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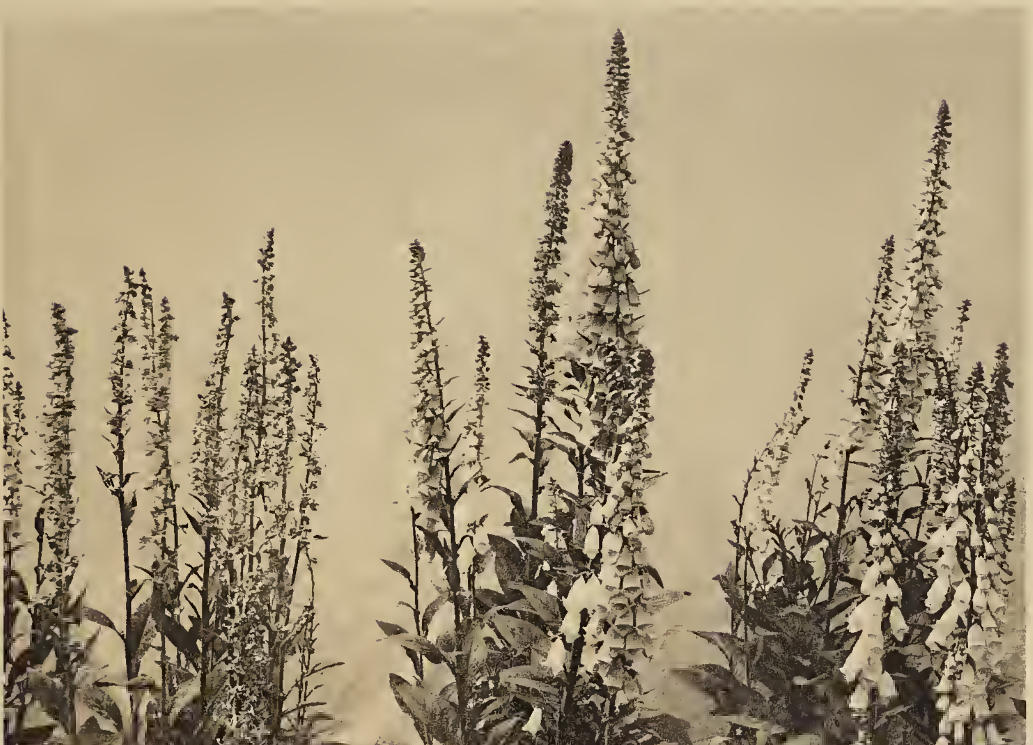
CORRIGENDA.

p. 208, line 15, for from *read* " form."

p. 208, line 11 from bottom, for uredospores *read* " aecidiospores."



SAUNDERS—MUTATION IN THE FOXGLOVE.

THE

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THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. Cavers, D.Sc.

[Figs. 55—72.]

VI. SPHAGNALES.

THE general vegetative characters of *Sphagnum*, the sole genus in this group, are, perhaps, too well known to require detailed treatment here. The stems, individually weak, gain support by their dense aggregation when growing, as is usual, in cushions above the surface of the water, the closely crowded branches at the top being either pale-green or showing various shades of red, yellow, or brown, while lower down the plants are brownish or dirty-white. The length to which the stems may grow is practically indefinite, and when the plants occur loosely in pools they may be several feet long. The branches arising from the main stem are of three kinds, without counting those which bear the antheridia and archegonia. At the apex of the plant the branches are short and so crowded as to form a compact head or "coma" (Fig. 55), but lower down they are spaced out in tufts on the stem, usually at every fourth stem-leaf, and each tuft may consist of from three to about eight branches. In one species (*S. monocladum*) the branches are single, and in a few cases there are more than eight branches in a tuft. In the submerged species and varieties, growing in bog pools, all the branches are similar in form and structure and spread out from the stem, but in other cases some of the branches of each tuft stand out (divergent branches) while the rest are longer and more slender and droop, lying close to the stem and covering it as with a loose mantle (Fig. 56). At intervals one of the branches in a tuft, instead of forming a divergent or pendent short branch, grows upwards, repeats the structure of the main stem, and reaches the same height as the latter.

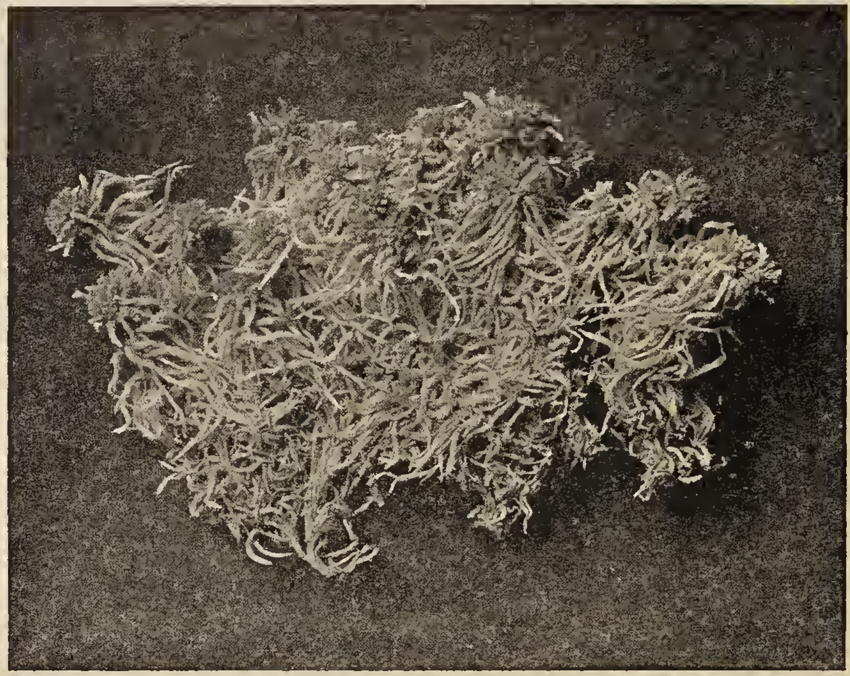

Fig. 55. Portion of a tuft of *Sphagnum acutifolium*, nat. size.

The stem, and each of its branches, grows by means of a three-sided apical cell (Fig. 57A), the segments becoming displaced very early from the three-rowed arrangement so that the leaves come to form usually five rows (Fig. 58). Each leaf grows for a time by a two-sided apical cell, from which new cells are cut off right and left in an extremely regular manner (Fig. 57C). In some cases, *e.g.*, in some submerged forms, the cells of the leaf remain practically uniform in size and shape, all containing chloroplasts, but as a rule this condition is rapidly replaced by differentiation of the cells into two sets. Some remain narrow but grow in length, and are arranged so as to form a network, each mesh of which is occupied by a large cell. The narrow cells retain their original contents, the large ones lose their protoplasm and chloroplasts. This differentiation takes place in a remarkably regular fashion. Each cell of the young leaf divides so as eventually to cut off a cell which is directed to the tip of the leaf and another which faces either the right or left side of the leaf; this is shown somewhat diagrammatically in Fig. 57E. where the dotted line represents the central axis of the leaf. The cells facing the apex (A) and the sides (R, L) remain narrow, while the third cell (H) of the triad grows in all directions and forms one of the large hyaline cells (Fig. 57F). As each cell divides in this symmetrical manner we get a regular and beautiful network of narrow green cells enclosing the large hyaline cells (Fig. 59). The latter have their walls thickened by ring-like bars, which are often joined up; these bars are thickest in the cells of the outstanding branches, and their thickness varies considerably according to the habitat, being greatest in plants growing in exposed or sunny places, while the fibres are feebly developed in plants growing in shade or in very wet places, and are often absent altogether in more or less

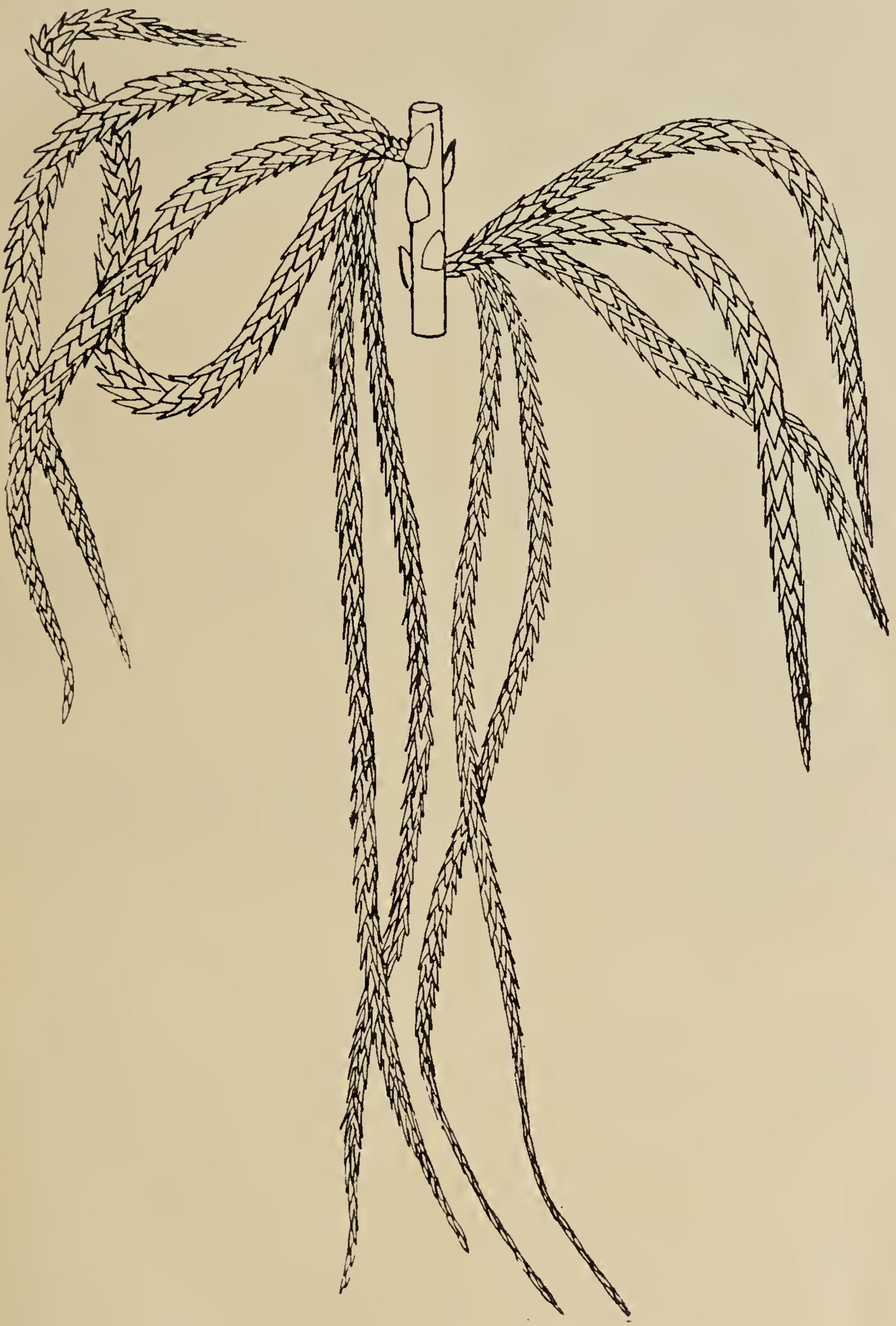

Fig. 56. *Sphagnum acutifolium.* Portion of a plant, showing two of the branch-tufts; in each tuft there are two drooping branches and three outstanding ones.

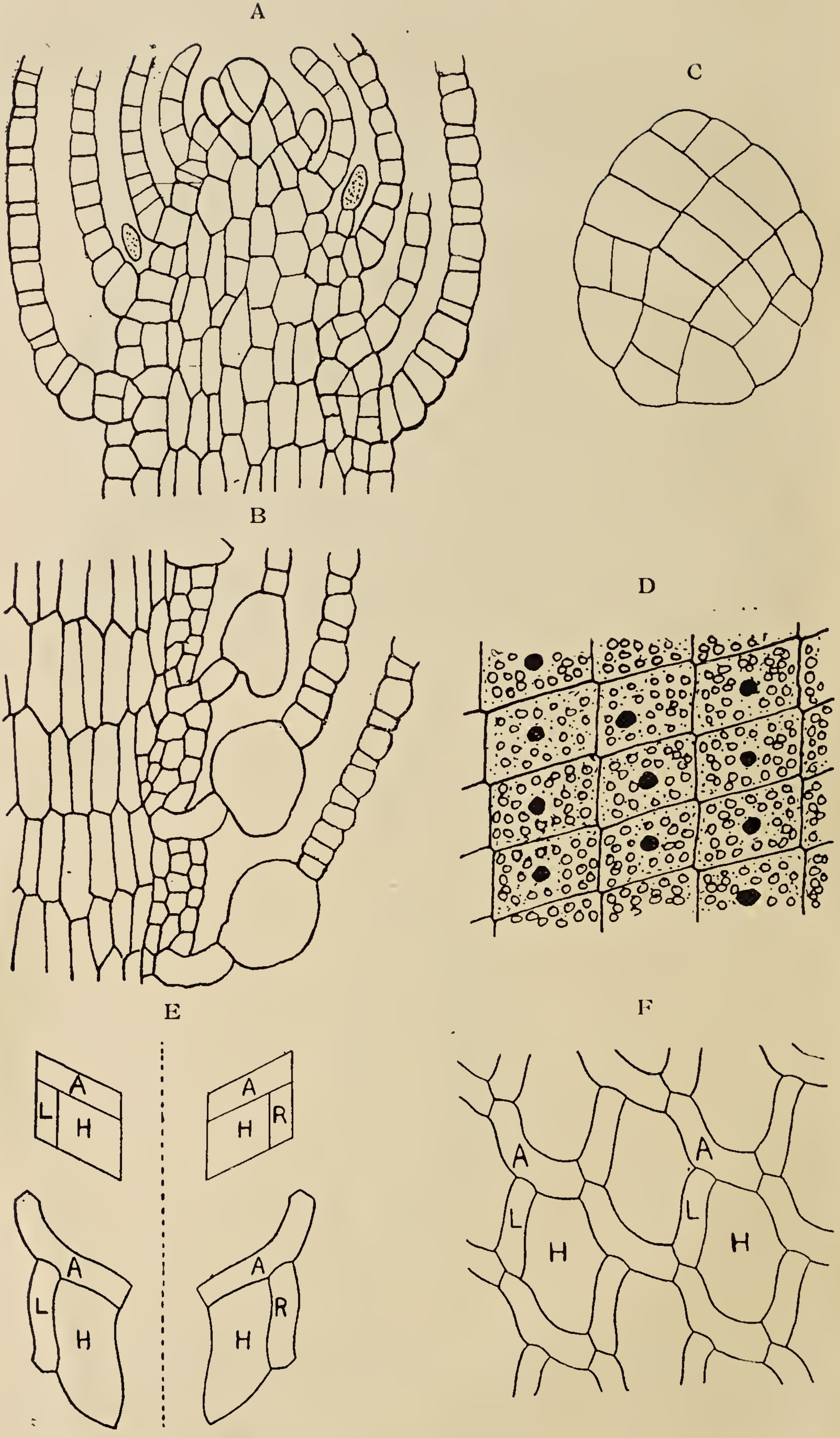

Fig. 57. *Sphagnum acutifolium.* A, median longitudinal section of apex of a stem, showing apical cell; B, similar section at some distance below the apex; C, a young leaf; D, cells from an older leaf; E and F, cells from older leaves, showing the division into triads (see description in text, pp. 2, 3).

submerged plants. In the leaves borne on the main stem, which are soon covered up by the pendent branches and therefore become functionless, the green cells soon lose their chlorophyll, while the walls of the hyaline cells become perforated with holes of irregular size and outline. In the branch-leaves, the hyaline cells have their walls perforated to a smaller extent and in a more regular manner, the pores being circular or oval and having a thickened rim; these pores generally occur at the points where three cells meet, though they are also found along the sides of the hyaline cells where these border on the green cells.

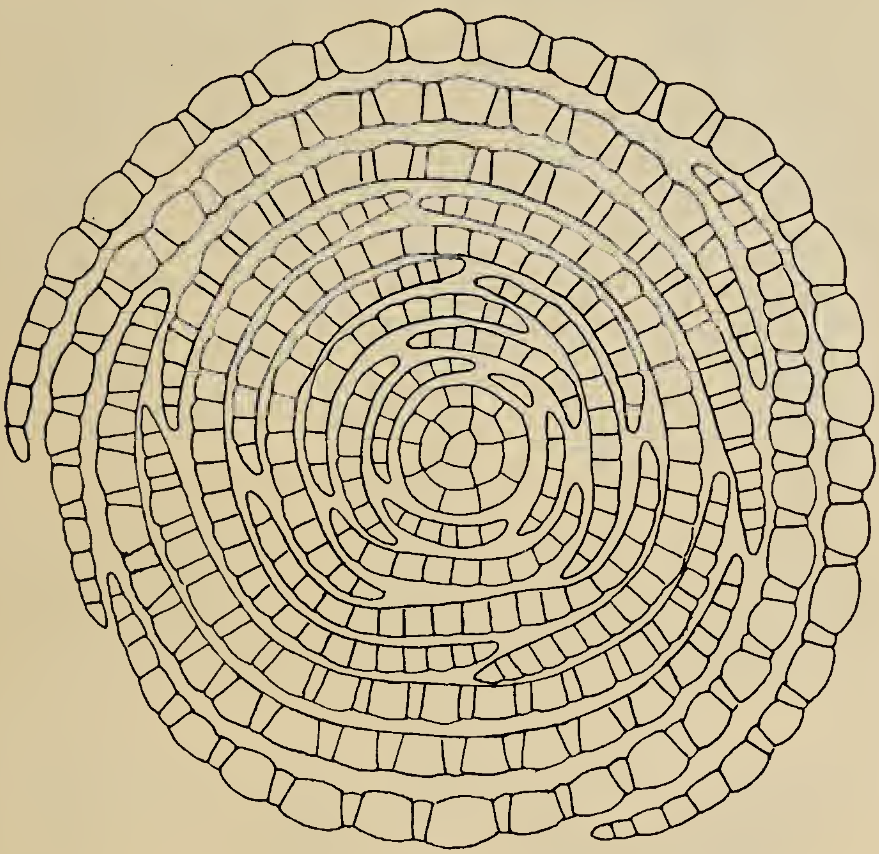

Fig. 58. Transverse section of growing-point of stem of *Sphagnum acutifolium*, showing in centre the apical cell and its youngest segments, and towards the periphery the differentiation of the leaf-cells.

At first a section across a young leaf shows that the cells, arranged in a single layer, are all rectangular and of about the same size, but later the cross-section shows an alternation of large hyaline and smaller green cells (Figs. 58, 59). In some species the hyaline cells bulge towards the underside of the leaf, the green cells being then triangular in cross section with the base of the triangle directed upwards and about flush with the upper side of the leaf. In other species the relation between the two kinds of cells is just the reverse of this; in others, again, the green cells are hemmed in above and below by the hyaline cells, and may be spindle-like in cross-section, their ends reaching neither the upper nor the lower side of the leaf. The classification of the Sphagna is largely based on the appearance of the two kinds of leaf-cells as seen in cross-section.

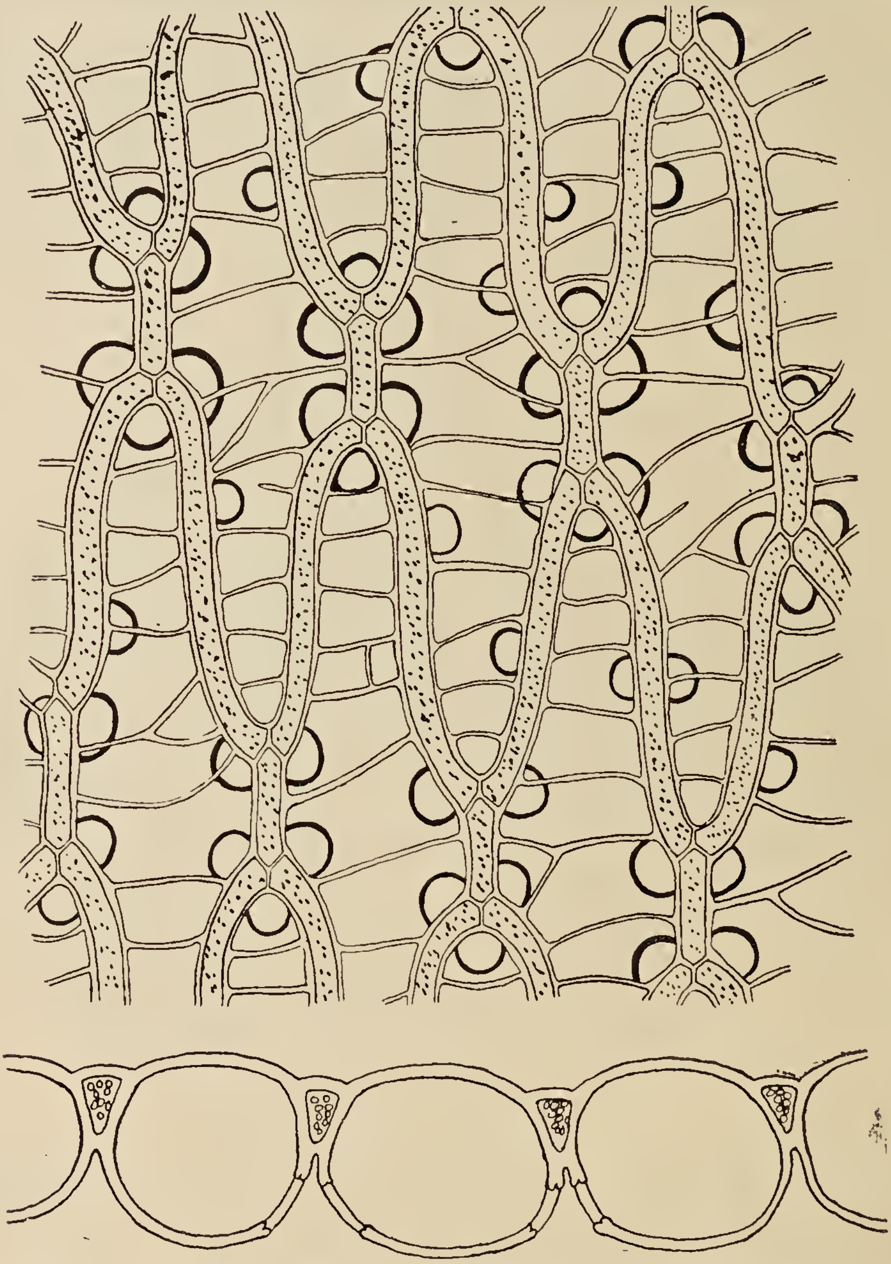
Fig. 59. *Sphagnum acutifolium*; the upper figure shows a portion of a mature leaf in surface view, the lower a portion of a transverse section of the leaf.

The inner tissue of the main stem consists of long cells sharply separated from an outer zone of short cells (Fig. 57B, Fig. 60). The latter (cortex) is at first a single layer, and in the branches it usually remains one cell thick, but in the main stem it often becomes four layers deep, its cells being large and colourless in most species. In submerged plants the whole stem consists of uniform tissue, all the cells except the innermost having chloroplasts—that is, in such plants the stem-tissue undergoes no differentiation and remains in the early stage, which is soon passed

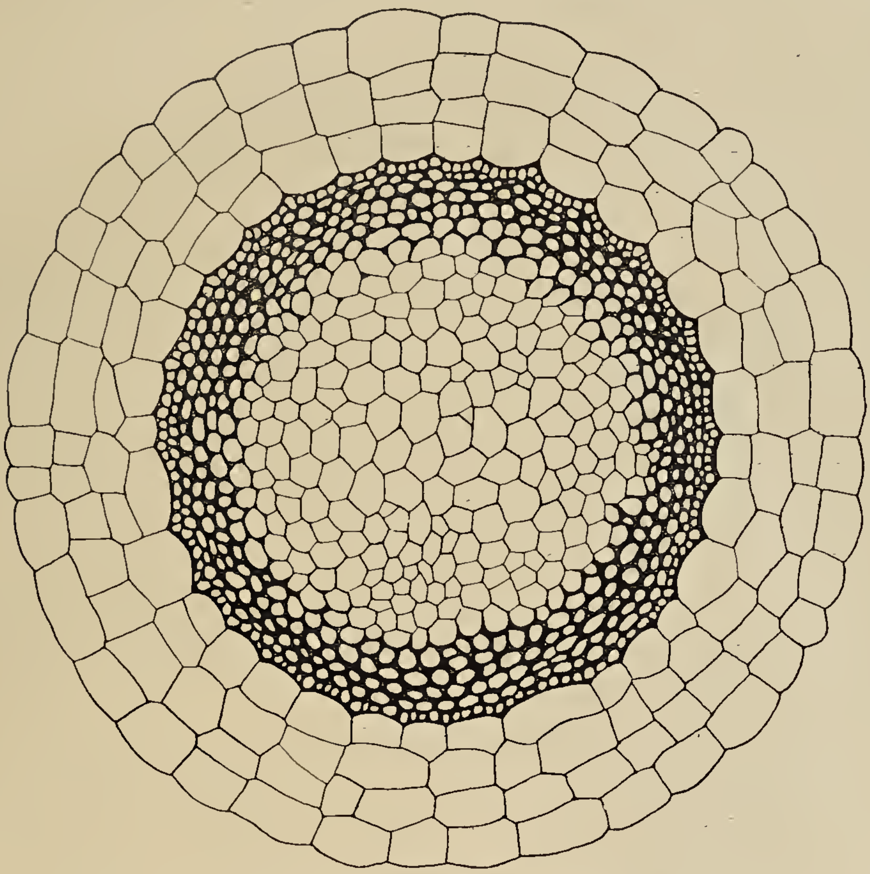

Fig. 60. Transverse section of stem of *Sphagnum acutifolium*.

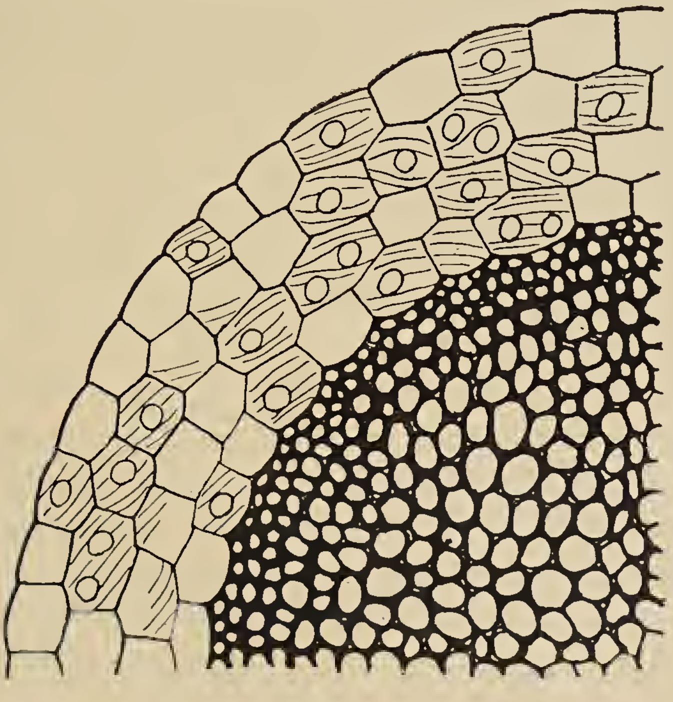

Fig. 61. Transverse section of stem of *Sphagnum cymbifolium*.

through in plants growing out of water. In a few species (*Sphagna cymbifolia*) the cells of the cortex resemble the hyaline leaf-cells in having strengthening fibres and pores on their walls (Fig. 61), but in most species these cortex cells are devoid of fibres and pores. The tissue within the cortex is differentiated into an outer zone of narrow thick-walled cells and a central region in which the cells are wider and shorter and have thinner walls. In the outer zone the long narrow cells have pits on the walls, but later the walls become uniformly thickened and the pits are obliterated. In the branches, of both the outstanding and the drooping types, some of the cells of the single-layered rind grow large and have their outer wall perforated at the upper end by a circular or oval hole, and as this end often projects outwards these cells resemble a bottle with a curved neck; these "retort-cells," which are especially conspicuous in *S. molluscum* (Fig. 62A), stand at one end of the insertion of a leaf, and they do not occur in the *Cymbifolium*-section, in which the cortex of both the main stems and the branches consists of perforated cells with fibrous thickenings.

Many inaccurate statements are found in text-books concerning the biology of *Sphagnum*. Oltmanns (24) was the first to make careful experiments on the remarkable capacity of *Sphagnum* for absorbing and giving off large quantities of water. In most species, the water is drawn up by capillary action, an extremely effective system of capillary spaces being formed by the drooping branches which hang down against the stem and overlap each other. If the tufts of branches be removed from the end of the stem, which is then dipped into water, the plant remains dry, hence the stem-tissue does not serve a conducting function. But in *S. cymbifolium* and its allies, in which the cortex cells have pores and fibres on the walls, the removal of the pendent branches does not stop the drawing-up of water, though even here water passes up much more rapidly when these branches are left intact; in these species no water ascends at all when both the pendent branches and the cortex are stripped from the end of the stem. As is well known, *Sphagnum* rarely grows on limestone soils. According to Paul (26, 27), calcium carbonate is very injurious to *Sphagnum*, even in small quantities; he grew various species in water containing lime and found that the plants soon perished. He states that not all salts of lime have an equally injurious effect, and that alkaline salts of potassium and sodium are as deleterious as those of lime. Various other writers have stated that the peat-mosses give an acid reaction on the surface, hence the injurious effects of calcium carbonate may be due to the neutralising of the acidity; that "Hochmoor" forms contain more acid than those growing on "Flachmoor" and that the former are more sensitive to lime; that on "Hochmoor," there is less mineral food available for the Sphagna in the sub-stratum, and that the amount of acidity and the sensitiveness to its neutralisation decrease as the amount of available mineral food increases; also that, in general, "Hochmoor" Sphagna absorb more water than "Flachmoor" Sphagna.

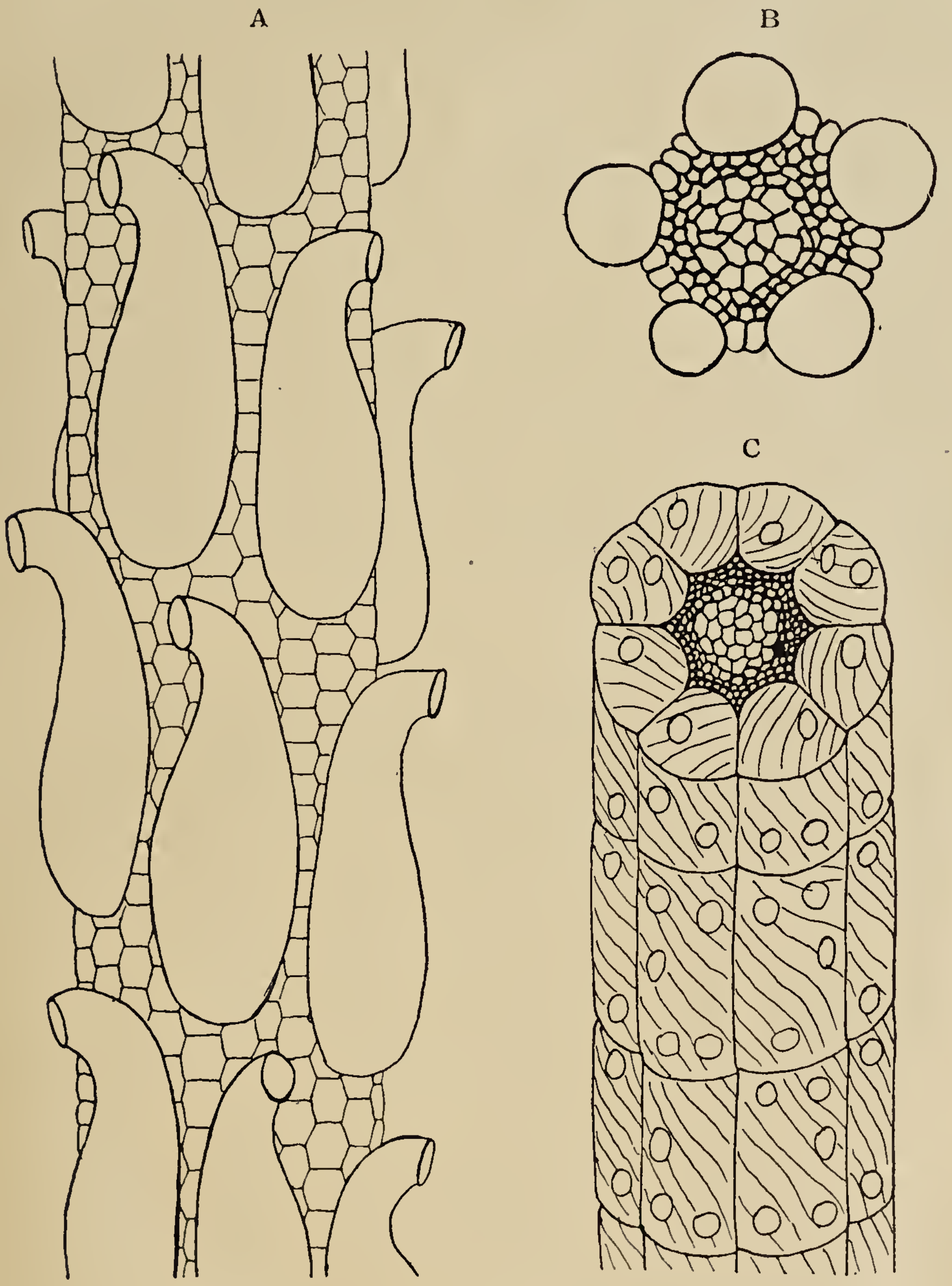

Fig. 62. A, portion of a branch of *S. molluscum*, after removal of leaves; B, transverse section of same; C, portion of a branch of *S. cymbifolium*.

Many interesting contributions to the physiology and ecology of *Sphagnum* are to be found in the papers of Peterfi (28), Sernander (46), and Timm (47), besides those of Oltmanns and Paul which have already been referred to; the earlier literature of the subject is given fairly fully by Paul in his 1908 paper. The writer has recently (4) given a summary of some of the more striking features in the biology and ecology of *Sphagnum*.

Since the sexual organs and sporogonium are practically uniform in the various species, the classification of *Sphagnum* is based entirely upon the vegetative organs, and it is at any rate easy to divide the genus into a small number of fairly natural groups, but beyond this point there is no general agreement among sphagnologists, some of whom have carried on controversies quite as spirited and even violent as those which have enlivened the history of lichenology; perhaps the best—or worst—instance is to be found in the wrangle between Röll and Russow regarding the constancy of species in the genus *Sphagnum*, in the course of which Röll called Russow "einen hartgesottenen verbohrten Art-Dogmatiker von der schlimmsten Sorte," and even worse things.

Apart from these somewhat barren and too often polemical discussions, it is generally admitted that the species of *Sphagnum* vary considerably, also that the different sections into which the genus has been divided show analogous variations. As was clearly pointed out by Jensen (8), the variations in the form of the Sphagna may be attributed to differences in the environmental conditions with regard to moisture, light, temperature, etc. The leaves are, naturally, the organs most liable to undergo variation, but the branching is also affected by these different conditions. Jensen distinguished three chief types of "analogous variation":—(i.) "formæ immersæ," growing submerged in water, with long stems, no distinct terminal head—the branch-tufts being widely separated owing to elongation of the stem—and with long leaves, the stem-leaves being similar in structure to the branch-leaves; (ii.) "formæ compactæ," growing in dry or cold habitats, in which the shoots are compact, forming low cushions, the branches short, and the leaves closely overlapping; (iii.) "formæ squarrosæ," growing in sheltered and shaded places, with robust shoots, leaves broad and deep green in colour. Other types are "laxæ," with the leaves widely spaced out; "tenellæ," with unusually long and slender branches and narrow leaves; "falcatæ," with falcate arrangement of the leaves at the curved tips of the branches. Jensen pointed out that in the *Sphagna acutifolia* and the *Sphagna subsecunda* we get a parallel series of forms showing the various types just mentioned, though the two groups are readily distinguished by the arrangement of the green and hyaline leaf-cells as seen in cross-section; while the *Sphagna cuspidata* and the *Sphagna cymbifolia* contain representatives of about half of the "analogous variation" forms. On the other hand, the *Sphagna compacta* are the least variable types, usually growing in relatively dry places and showing a very limited range of biological forms, nearly all being compact, though squarrose and submerged forms sometimes occur in this group.

The growth of a *Sphagnum* shoot shows a more or less marked annual periodicity, though in winter it is not brought to a standstill unless the temperature falls to freezing point. The laying-down of new branches at the apex proceeds during the whole period of active growth (spring and summer), but the elongation of the stem becomes arrested in late summer or early in autumn. While the stem is lengthening, the outermost (oldest) of the branches forming the cushion-like top of the plant are continually being carried downwards and spaced out in tufts on the stem. Among the later branches formed in autumn are the male and female branches, which may either occur on the same plant or on different plants—most of the British species are diœcious, but some show either condition quite indifferently. The male branches are formed earlier than the female, and are carried down on the stem as the latter elongates, while the female branches arise later and are found during winter and spring on the upper part of the plant, but later are carried downwards as the stem lengthens. The sexual organs usually mature in late autumn and winter, and may be found fully developed in mid-winter, even when the plants are covered by snow. Fertilisation usually occurs in early spring; the young sporogonia may be found as early as February, and the ripe capsules shed the spores from about July to September.

The male branches are at first indistinguishable from the ordinary divergent branches of a tuft, but later they acquire a characteristic appearance. One or more of the branches of a tuft expand and become catkin-like, and above this swollen antheridium-bearing region taper again to a pointed tip which may continue to grow like an ordinary branch, giving the "catkin" a spindle shape. The leaves that protect the antheridia resemble ordinary branch-leaves in structure, but are usually shorter, more closely overlapping, arranged in regular straight or spiral rows, and often richly coloured red, purple, brown, etc., even in species where the ordinary branches are devoid of colouration other than pale green. The antheridia are spherical and attached to the axis of the branch by a slender and relatively long stalk which is inserted at one end of the base of the leaf. The position of the antheridia with reference to the leaves is thus the same as that on a branch of a stem, and Leitgeb (10) noticed that a vegetative bud may occupy the place of an antheridium on the male branch, The branching filaments, described by Schimper in his classical work on *Sphagnum* (44) as paraphyses accompanying the antheridia, are only of occasional occurrence, and they probably belong to the fungus which will be mentioned later in connexion with the archegonia and sporogonia. The antheridium arises from a cell which after repeated transverse divisions, producing a cell row, shows apical growth by means of two sets of segments cut from the terminal cell; the lower cells divide longitudinally, as well as transversely, to form the thin stalk.

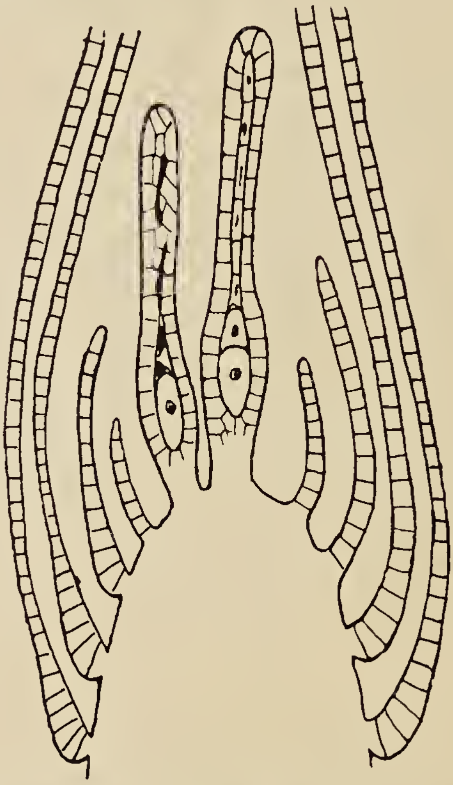

Fig. 63. Longitudinal section of female branch of *S. compactum*, showing two archegonia.

The female branches are very short and bud-like, deep-green in colour. The leaves externally visible at the top of the branch are usually much longer than any other leaves on the plant; they differ from the branch-leaves in having few fibres in the hyaline water-cells, and from the stem-leaves in having abundant chlorophyll. The structural peculiarities of these leaves are obviously connected with their functions, the protection and nutrition of the developing sporogonium; owing to the scarcity of fibres in the cells, these leaves closely invest the young fruit instead of being stiff or curved outwards, and their abundant chlorophyll enables them to carry on active photosynthesis. Within the large enveloping leaves we find at the apex of the branch a small group of archegonia surrounded by a number of small leaves which for a long time remain in an embryonic or undifferentiated condition (Figs. 63, 64). The first archegonium is formed from the apical cell of the branch, and then from two to four others are developed around it; occasionally there are only two archegonia, or no more

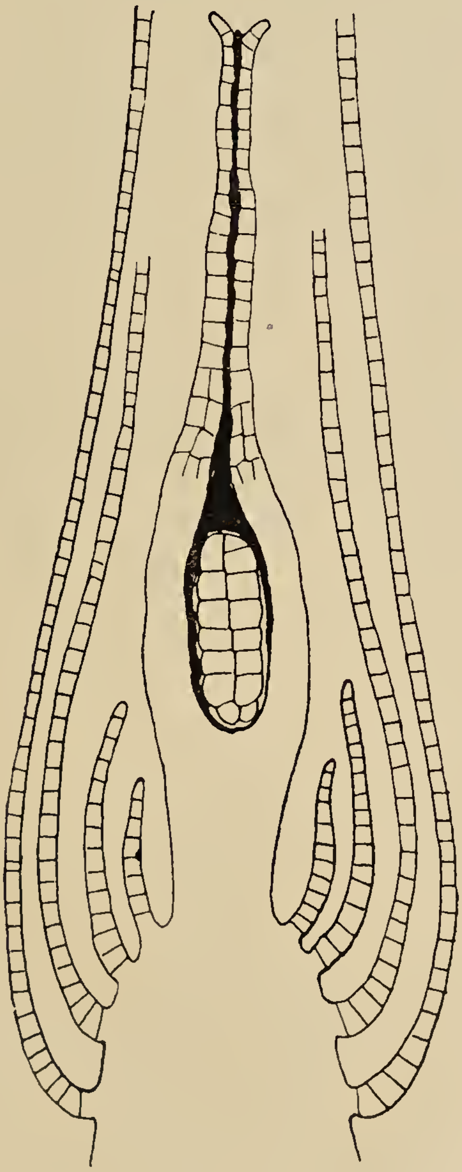

Fig. 64. Longitudinal section of female branch of *S. compactum*, showing fertilised archegonium with embryo.

at all may be produced after the first one. The archegonium resembles that of the Bryales in structure; it has a thick stalk and the neck-cells are in spiral rows. It has not been determined with certainty whether it grows by means of an apical cell, as in Bryales.

The embryogeny of *Sphagnum* presents some interesting features. The first division of the fertilized egg is into an upper (epibasal) and a lower (hypobasal) cell, but the further development differs from that seen in Bryales and recalls the embryogeny of the Jungermanniales; the hypobasal cell undergoes a few irregular divisions, while the epibasal cell divides repeatedly by transverse walls to form a row of about six cells (Fig. 65). As in Jungermanniales, each of these cells divides into quadrants and then by tangential divisions a series of inner cells (endothecium) is separated from a layer of outer cells (amphithecium). The embryo soon becomes pear-shaped (Fig. 66), the narrow upper portion eventually producing the capsule, while the lower portion for a time grows much more rapidly and forms the swollen haustorium; at this stage the embryo strikingly resembles that of Anthocerotales, except for the absence of the meristem zone. The archesporium is dome-shaped and arises, as in Anthocerotales,

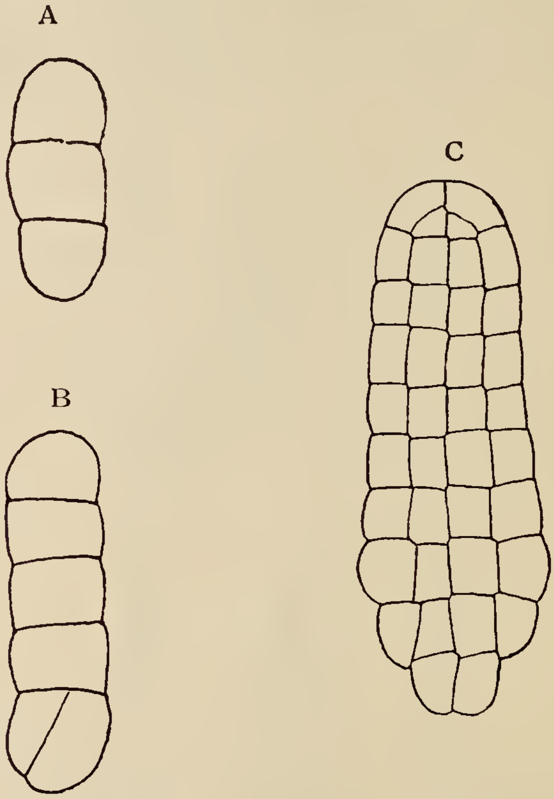

Fig. 65. *Sphagnum compactum.* Three stages in development of embryo sporophyte.

from the inner layer of the amphithecium, the endothecium of the capsule forming the sterile columella. The archesporium soon becomes four-layered, and the cells adjoining it on both sides divide so as to form a small-celled spore-sac layer, as in Bryales. The stalk of the fertilised archegonium expands as the haustorium bores down into it and into the underlying tissue of the stem, the lower part of the venter also stretching to keep pace with the growth of the capsule, while the withered neck and upper portion of the venter are carried up on the surface of the calyptra.

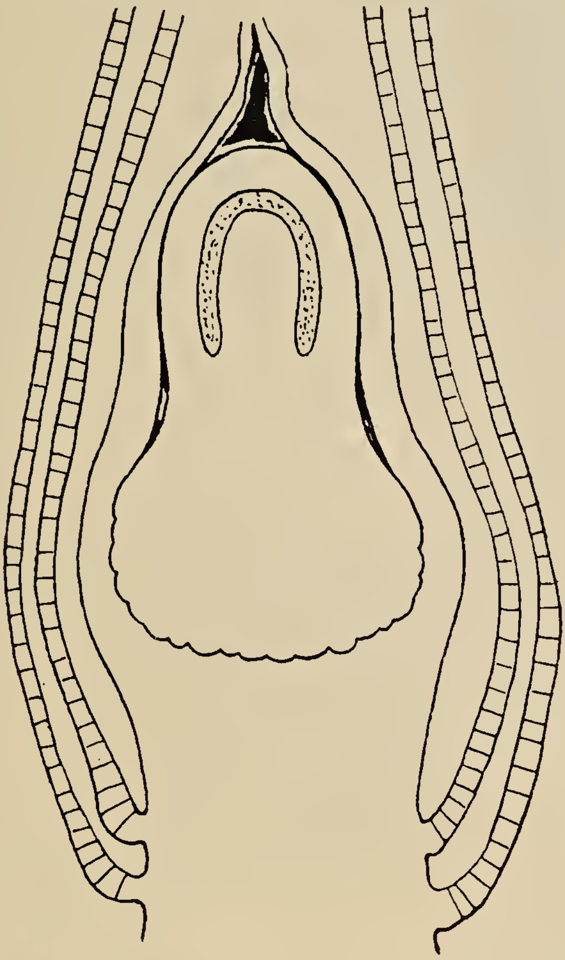

Fig. 66. *Sphagnum compactum*; later stage in development of sporogonium.

Chlorophyll is present in the developing capsule, especially in the tissue lying outside of the spore-sac and in the small cells of the spore-sac itself. As the capsule matures, the cells of the superficial layer acquire thickened and brown coloured walls, forming a well defined epidermis ; along a circular transverse line near the top of the capsule these cells remain small, forming the groove-like annulus and delimiting the lid by which the capsule eventually dehisces (Fig. 67, Fig. 68 c). The epidermis shows numerous rudimentary stomata, which begin to develop like those on the

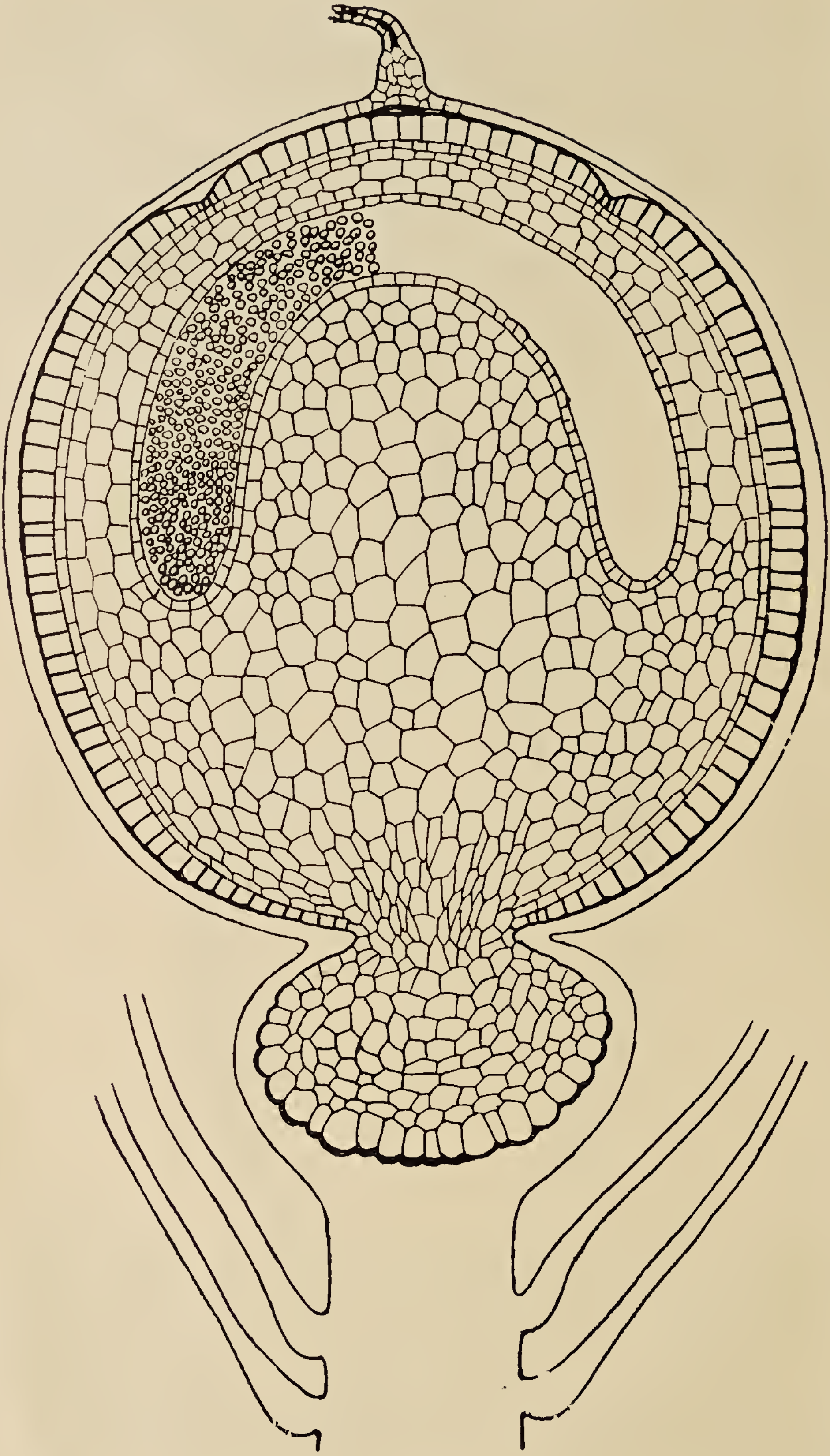

Fig. 67. Longitudinal section of a nearly ripe sporogonium of *S. compactum*. At the top is the withered neck of the archegonium, the lower part (calyptra) of which covers the nearly spherical capsule. The capsule-wall shows the groove which separates off the lid. The dome-like spore-sac (spores only shown on left side), and the central tissue (columella) are seen. The capsule is connected by a constriction with the absorbing foot. Elongation of the pseudopodium has not yet taken place.

apophysis of many Bryales, an isolated epidermal cell remaining thin-walled and dividing into two "guard-cells," but the partition-wall not splitting to form a pore (Fig. 68 A, B.) The ripe capsule is raised on a "pseudopodium," formed by elongation of the upper part of the axis of the female branch, the uppermost leaves of which become slightly separated, though the growth is greatest between these leaves and the sporogonium itself, so that the pseudopodium has a smooth surface and consists of elongated cells; the top of this apparent seta is occupied by the bulbous haustorium, which is separated from the capsule by a neck consisting of narrow pitted cells. The calyptra is ruptured irregularly by the slight expansion of the ripening capsule; leaving a cup-like sheath; sometimes the rupture is transverse, so that the upper portion of the calyptra is pushed up like a cap, tipped by the archegonium neck, on the top of the capsule.

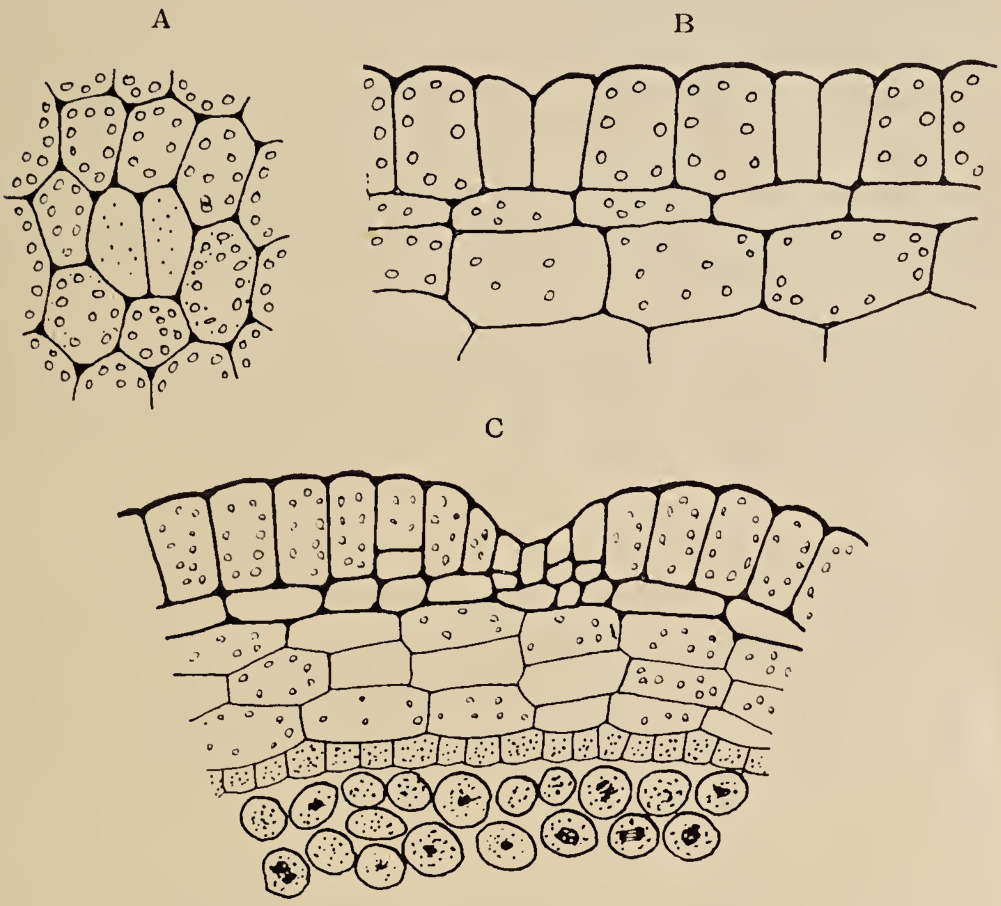

Fig. 68. *Sphagnum acutifolium.* A, stoma in surface view; B, part of longitudinal section of capsule, showing two stomata; C, part of longitudinal section showing the annulus and part of the spore-sac, with developing spores.

Among the archegonia, as well as the antheridia, branching filaments sometimes occur, which were regarded by Schimper as paraphyses serving to keep the sexual organs moist. Doubt was thrown upon this observation by Leitgeb (8), who investigated the development of the antheridia, and by Waldner (49), who worked out the embryology of the sporogonium; in fact, neither of these writers could observe such threads at all. Schimper and other observers also noticed that the capsule sometimes contains very small spores which to a greater or less extent replace the ordinary spores. Schimper described these "microspores" as arising from the ordinary spores by repeated division, and Warnstorf suggested that *Sphagnum* is a heterosporous Bryophyte, the microspores producing male plants and the large spores female plants! However, Nawaschin (20, 21) showed that the filaments and the "microspores" belong to a parasitic Fungus—*Tilletia Sphagni*—the life history of which he worked out, tracing the entrance of the mycelium into the developing capsule and its ramification through the archesporium, where it produces its own spores, mingled with those of *Sphagnum* or even, in small and deformed capsules, replacing them altogether.

The dehiscence of the capsule is brought about by a curious and probably unique mechanism. It was long ago noticed that the capsule of *Sphagnum* explodes with a cracking or "popping" noise, the shape of the capsule suddenly changing from spherical to cylindrical, and the lid, together with the spores, being thrown out to a distance of several inches. The beautiful mechanism involved was explained by Nawaschin (22). As the ripe capsule dries, the delicate central tissue (columella) shrivels and is replaced by air, so that the capsule eventually contains, within the brown epidermal layer, practically nothing except the spore-sac (by this time an inverted saucer-like bag within which the spores lie loosely) and below this a relatively large air cavity. As drying proceeds, the longitudinal diameter of the capsule remains unchanged, but the transverse diameter is greatly shortened owing to transverse contraction of the epidermis, and the imprisoned air is therefore compressed. During this change, the lid (firmer in texture than the rest of the wall) shrinks but little, a difference in tension is thus set up, and finally the lid becomes loosened along the annular groove and is forcibly shot off, along with the spores, in exactly the same way as a bullet from an air-gun. Nawaschin's paper (22), should be consulted for details of his ingenious experiments and his determination of the volume and pressure of the air in this remarkable "pop-gun" capsule.

The protonema of *Sphagnum* differs from that of most other

Mosses. The germ-tube given out by the spore is soon converted, by growth of its end-cells, into a flat discoid thallus, forming an irregularly lobed expansion one cell in thickness, attached by numerous rhizoids. The protonema may reproduce itself by sending out from its margin threads which give rise to discs, and these may later become separated as independent protonemata. Usually one leafy *Sphagnum* plant arises from each protonema, as a projection formed by active growth and division of a marginal cell at the base of the protonema; in this cell arise walls cutting out a three-sided apical cell, the segments cut out from this at once producing the young leaves. The fourth or fifth leaf shows the differentiation into green and hyaline cells; at first this differentiation is shown only in the lower portion of the leaf, the upper cells remaining uniform and green.

Oehlmann (23) has shown that *Sphagnum* plants are able to produce protonemata and young leafy plants from practically any living portion of the mature gametophyte. The young *Sphagnum* plant, whether arising from primary protonema (produced on germination of the spore) or from secondary protonema (in regeneration of portions of the mature plant) bears rhizoids which may twine like tendrils around old *Sphagnum* stems and other supports; but as the plant developes it produces no more rhizoids, these absorbing hairs being unnecessary since the plant has such efficient means of absorbing water in its remarkable capillary system and its perforated hyaline cells.

The affinities of *Sphagnum* will be discussed later, when the characters of the Andreæales and Bryales have been dealt with.

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VII. ANDREÆALES.

[Fig. 69].

THIS group is represented by the single genus *Andreæa*, which is in various respects intermediate between the Sphagnales and the Bryales, especially in the structure and development of the sporogonium. There are about 100 species of *Andreæa* distributed over the whole earth, but especially abundant in the colder temperate regions, though found on the higher mountains in the tropics. They are small plants, which creep and branch sympodially, forming dark brown or black tufts, and growing especially on siliceous rocks in exposed places—though two New Zealand species grow on wet stones in streams.

The mature stem and leaf hardly differ in structure from those of various Bryales. The stem tissue is practically uniform, there is no definite conducting strand; the leaf usually consists of a single layer of cells, but in some species has a midrib. From the basal creeping portions of the stem there spring numerous rhizoids, mostly consisting of cylindrical or plate-like outgrowths, the former growing into the rock crevices, while the latter become applied closely to the rock surface.

The sexual organs are borne in terminal groups on separate branches, usually on the same plant; each group is surrounded by a number of large involucral leaves, and among the antheridia and archegonia there are numerous filamentous paraphyses. The development of the sexual organs was worked out by Kühn in his fine memoir on the genus (3), and apparently *Andreæa* shows close resemblance to the Bryales in the general characters of these organs. The mature antheridium has an ellipsoid body and a relatively long stalk, the latter consisting of two rows of cells and having a dilated base.

The sporogonium of *Andreæa* presents a curious mixture of characters, some of which are peculiar to the genus, while others recall the structural and embryological features of the sporophytes of Sphagnales and of Bryales. After the formation of the transverse basal wall, the divisions in the hypobasal cell are irregular, but the epibasal cell divides at once by oblique walls which cut out a two-sided apical cell. According to Waldner (4), who worked out the early stages in detail, the apical cell cuts off, as a rule, about six segments on either side before further divisions occur in the segments. Each segment is first divided by a radial wall, and then tangential walls are formed which separate a central group (endothecium) of four cells from an outer layer (amphithecium) of eight cells, as seen in cross section of the embryo. In the upper segments—beginning with third oldest, and extending through three or four segments above this one—the archesporium is formed as a layer of cells cut from the endothecium, the central portion of which forms the columella, while the ampithecium gives rise to the capsule-wall. The archesporium becomes two-layered, and is dome-shaped, extending over the top of the columella, as in *Sphagnum*. The two lowest epibasal segments contribute to the foot; those above the archesporium produce the sterile tip of the capsule (see Fig. 69, A to J).

The ripe capsule is ovoid in form, having a very short seta or neck connecting it below with the somewhat swollen foot or haustorium. The capsule-wall consists of about six layers of cells, at first containing chloroplasts; the epidermal cells are thick-walled over the greater part of the capsule, but along four longitudinal lines which are equidistant from each other and reach neither the apex nor the base of the capsule—these lines are laid down at a very early stage and doubtless correspond to the primary quadrant divisions in the archesporium-forming cells of the embryo—the epidermis cells have thin walls and divide tangentially so as to form two superposed rows (Fig. 69, M, N).

The venter of the fertilised archegonium grows actively, forming the calyptra and becoming about six cells thick; after a time, when the capsule is nearly mature, the calyptra is ruptured and its upper portion is carried up on the apex of the capsule. As in *Sphagnum*, the axis of the archegonial shoot grows up as a psuedopodium, carrying on its surface some of the unfertilised archegonia, and expands above into a swelling in which the sporogonial haustorium is embedded (Fig. 69, K, L). When the ripe capsule dries, dehiscence occurs along the four longitudinal lines marked out by the rows of thin-walled epidermis cells already noted. In most cases the capsule opens by four slits, extending neither to apex nor base of capsule, but in some species there are from six to eight slits; while in *A. Wilsonii* (a South American species) the capsule is said to open by slits that reach the apex and extend only a short distance downwards, so that the whole tip of the capsule splits into from four to eight teeth. Unfortunately, the species just named has not been fully investigated; careful exami-

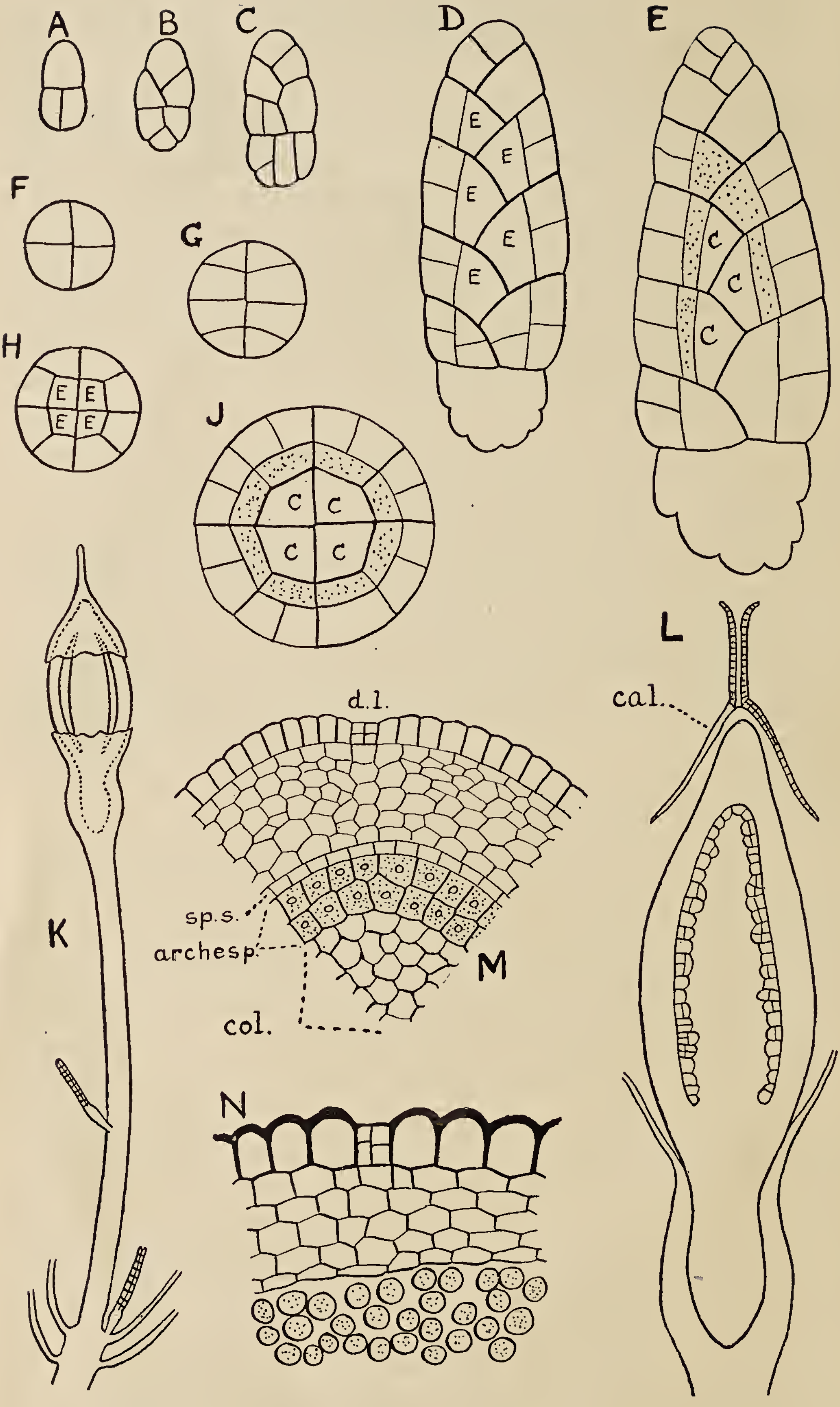

Fig. 69.—*For description see next page.*

Fig. 69. *Andreæa.* A to C, stages in development of the embryo sporophyte, in longitudinal section; F to J, similar stages in transverse section; K, diagrammatic view of the entire sporogonium after elongation of pseudopodium and transverse rupture of the venter of the fertilised archegonium; C, longitudinal section of fairly advanced sporogonium, showing the archesporium, calyptra, and vaginula, also the upper portion of the pseudopodium in which is inserted the foot of the sporogonium; M, part of a transverse section of a fairly advanced sporogonium, showing one of the dehiscence lines in the epidermis of the capsule-cell; N, similar section of a ripe sporogonium. All the figures are somewhat diagrammatic; *c.*, *col.*, columella; *cal.*, calyptra; *e.*, endothecium; *d. l.*, dehiscence line; *sp. s.*, spore-sac.

nation of fresh or suitably preserved material would be of great interest, in order to determine whether or not we have here a transition from the peculiar dehiscence mechanism of the typical Andreæales to that seen in *Tetraphis.* As shown by Goebel (2), the moist spores adhere to the edges of the slits, which close in wet weather, and become dry and loosened when the slits gape on drying.

The germination of the spores and the peculiar forms of the protonema were investigated by Kühn and also by Berggren (1). The spore begins to germinate and forms a cell-mass before the exospore is ruptured; when rupture occurs, the superficial cells of the mass grow out separately to form filaments which grow apically, segments being cut off from the terminal cell by transverse walls. These filaments branch freely, some of the branches creeping over the substratum, while others grow upwards and turn green, others again growing into crevices in the rock and remaining colourless. The erect filaments may become cylindrical and produce flat leaf-like plates, hence the forms of the protonema are very diverse, and any of them may produce buds which grow into leafy shoots. Elaborate protonemata of a very similar kind occur, however, in various Bryales.

LITERATURE OF ANDREÆALES.

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2. Goebel, K. "Ueber die Sporenausstreuung bei den Laubmoosen." Flora, 1895; 27 pp.
3. Kühn, E. "Zur Entwickelungesgeschichte der Andreæaceen." Schenck and Leurssen's Mitt. a. d. Gesammtgebiete d. Bot., Band I., 1870; 56 pp.
4. Waldner, M. "Die Entwickelung der Sporogone von *Andreæa* und *Sphagnum.*" Leipzig; 1887.

The genus *Andreæa* is also dealt with by Goebel (Organography), Lotsy (Vorträge, Band 2), Campbell (Mosses and Ferns), and in Engler and Prantl (Nat. Pflanzenfam.).

VIII. BRYALES.

[Figs. 70—72.]

OMITTING for the present the vegetative characters, the three groups of higher Bryophytes or Mosses may be thus distinguished:—

I. **Sphagnales.** Embryo sporophyte first divides into a row of several cells, by formation of repeated transverse walls in the epibasal cell; haustorium formed by growth and division of hypobasal cell; further growth of epibasal half intercalary; archesporium produced chiefly from the innermost layer of the amphithecium; the endothecium forms only the columella, except at the apex, where it contributes to the production of the dome-like archesporium; mature sporogonium consists of a spherical capsule and a bulbous haustorium, the two being separated by a constriction: capsule carried upwards by elongation of female shoot axis to form a pseudopodium, and opening by a lid.

II. **Andreæales.** Epibasal cell divides by inclined walls cutting out a two-sided apical cell, by which growth is effected for some time (until the differentiation of the archesporium); hypobasal cell divides irregularly; haustorium formed by hypobasal half and lowest segments of epibasal half; archesporium produced chiefly by the outermost layer of the endothecium, the inner portion of which forms a columella; archesporium dome-shaped, being completed above by the inner tissue of the amphithecium, and therefore covering the apex of the rod-like columella; mature sporogonium carried upwards by a pseudopodium; capsule opens by four longitudinal slits, which typically reach neither apex nor base of capsule.

III. **Bryales.** Epibasal and hypobasal halves of embryo usually both grow by a two-sided apical cell; the haustorium, separated from the capsule by a longer or shorter seta, is developed chiefly from epibasal cell; archesporium arises in the outermost layer of the endothecium (in *Archidium* from the entire endothecial tissue) and is a tubular zone, hence the columella extends into the apex of the capsule; ripe capsule usually opens by a lid, which in the higher types is detached by the separation of a ring of special cells and not merely by splitting of cell-walls, and a special mechanism (peristome), which ensures gradual spore-dispersal, is usually present and is typically developed from the inner amphithecial tissue lying above the archesporial region of the capsule.

These three groups are closely connected with each other, and sharply separated in many respects from the lower Bryophytes. The three "Moss" groups agree closely in the vegetative characters of the gametophyte, in the growth of the young archegonium by means of an apical cell, and in the absence of sterile cells or elaters from the archesporium.

The Bryales, by far the largest group of Bryophyta, present extraordinary uniformity in the early development of the sporogonium and the mode of origin of the sporogenous tissue. Comparatively little work has been done on the embryogeny of the group, but it would appear that in general the archesporium arises from the outermost zone of the endothecium, and the outer spore-sac from the innermost zone of the amphithecium, the characteristic air-space of the Bryinean capsule being formed between the outer amphithecial tissue (which produces the capsule-wall) and the outer spore-sac, while the inner spore-sac consists of a layer of cells cut off from the inner side of the primary archesporial layer. The only outstanding exception to this general and probably universal mode of origin of the sporogenous tissue is that seen in the genus *Archidium*; here the air-space is formed as in typical Bryales, but there is no definite archesporium, unless we regard the entire endothecium as representing the archesporium; at any rate, there is no differentiation into columella and archesporium proper, and a few of the endothecial cells become spore-mother-cells, the sterile cells among which the fertile cells are scattered being absorbed during the maturation of the spores. In *Ephemerum* the embryogeny follows the normal Bryinean type, but the central sterile tissue of the endothecium produces a relatively feeble columella, which in some species disappears before the capsule reaches maturity. In the allied genus *Nanomitrium*, the slender columella is used up in the ripening of the spores, but the capsule has a zone of cells which form a rudimentary annulus and delimit the upper portion of the capsule as an operculum.

The primary division of the Higher Mosses into Cleistocarpi (capsule opening by irregular rupture or by decay of its wall) and Stegocarpi (capsule opening by a predetermined dehiscence line or zone which throws off the apical portion of the wall as a lid or operculum) appears to have been first proposed by Müller in 1849, and it has been maintained by the majority of bryologists to the present day, as has also the division of the Stegocarpi into Acrocarpi and Pleurocarpi (according to the position of the archegonial group, and therefore of the sporogonium, at the end of the main axis or that of a short lateral branch) which was made by Bridel in 1826. On various grounds, neither of these distinctions can now be regarded as forming a sound basis for the classification and phylogeny of the Bryales. Lindberg in 1879 distributed the cleistocarpous forms among the various stegocarpous families, to which he attached them according to their general resemblances apart from the absence of a lid. The cleistocarpous Bryales are mostly very small plants, often with the protonema persistent and more conspicuous than the leafy gametophyte and with the seta short or almost absent; the capsule wall at maturity consists usually of a single layer of cells, though (except in *Nanomitrium*) bearing stomata; and in some of the forms placed in this group there is a rudimentary annulus (*Nanomitrium*) and even a rudimentary peristome (*Mildeella*), though in the latter case this organ is functionless, since the rudimentary operculum does not become detached. Excepting *Archidium*, such of these cleistocarpous types as have been investigated (*Ephemerum*, *Pleuridium*, *Phascum*, *Nanomitrium*) show the typical Bryinean embryogeny. Much more detailed work on the cleistocarpous forms appears to be required before one can venture an opinion on the vexed question whether they are primitive forms, lying at the starting-point of several lines of development leading up to the typical Bryales, or on the other hand degenerate forms derived by reduction from various distinct groups of the stegocarpous Bryales.

The old distinction into Acrocarpi and Pleurocarpi must be abandoned, for many reasons. Many pleurocarpous forms occur among such acrocarpous families and genera as Leucobryaceæ, *Fissidens*, *Pleuroweisia*, etc.; not only do different species of the same genus differ in this respect, but in some cases the same plant may be both pleurocarpous and acrocarpous, *e.g.*, species of *Daltonia*, *Fissidens*, *Hypopterygium*. The division of the stegocarpous Bryales into Acrocarpi and Pleurocarpi is not only quite artificial, but it completely obscures the phylogeny of the group, for there can be no doubt that the pleurocarpous forms have arisen independently from various acrocarpous groups—a line may be traced, for instance, from the acrocarpous Orthotrichaceæ through intermediate forms like the Hedwigiaceæ and Cryphæaceæ to such typically pleurocarpous forms as *Eurhynchium* and *Hylocomium*, while another line leads upwards from the Bartramiaceæ to the Spiridentaceæ. Moreover, the characters of the peristome are practically identical in detail, as well as in the general structural plan, in such families as the Bryaceæ and Hypnaceæ, which, on the generally accepted classification, are widely removed from each other.

The most striking feature in the organisation is the evolution of the peristome, and it is upon the characters of this organ that something approaching a natural classification must be founded. Here again much remains to be done on the developmental side, for there are many gaps in our knowledge of the origin of the peristome and the annulus, despite the excellent memoirs of Lantzius-Beninga, Philibert, Goebel, Dihm, and others. Moreover, as pointed out by Loeske (31) in his recent interesting book on the Morphology and Classification of Mosses, welcome aid in the attempt to trace out the main lines in the evolution of the Bryales may come from practically every piece of research undertaken on the histology, physiology, and ecology of the various families, and there is room for careful monographs of many of the orders and genera.

Detailed treatment of the Bryales would unduly extend the scope of the present series of articles, and must therefore be left over for another occasion, but in order to draw together some of the more important results of recent work a brief summary will be given regarding the phylogeny of the Bryales. In this group we can distinguish four sharply marked types of peristome-structure, upon which it is probably justifiable to split up the higher Mosses into four independent series co-ordinate with the Sphagnales and Andreæales. The division suggested here is a compromise between the systems recently proposed by Lorch (32) in his fine monograph of the Polytrichaceæ, and by Fleischer (14) in his great work on the Mosses of Java. According to Lorch, the Bryales should be broken up into the four groups Polytrichales (Polytrichaceæ and Dawsoniaceæ), Buxbaumiales (*Buxbaumia*), Diphysciales (*Diphyscium*), and Bryales (or Eu-Bryales). Fleischer, on the other hand, unites the Buxbaumiaceæ and Diphysciaceæ into one group (Buxbaumiineæ), and splits off the Tetraphidaceæ as a second group

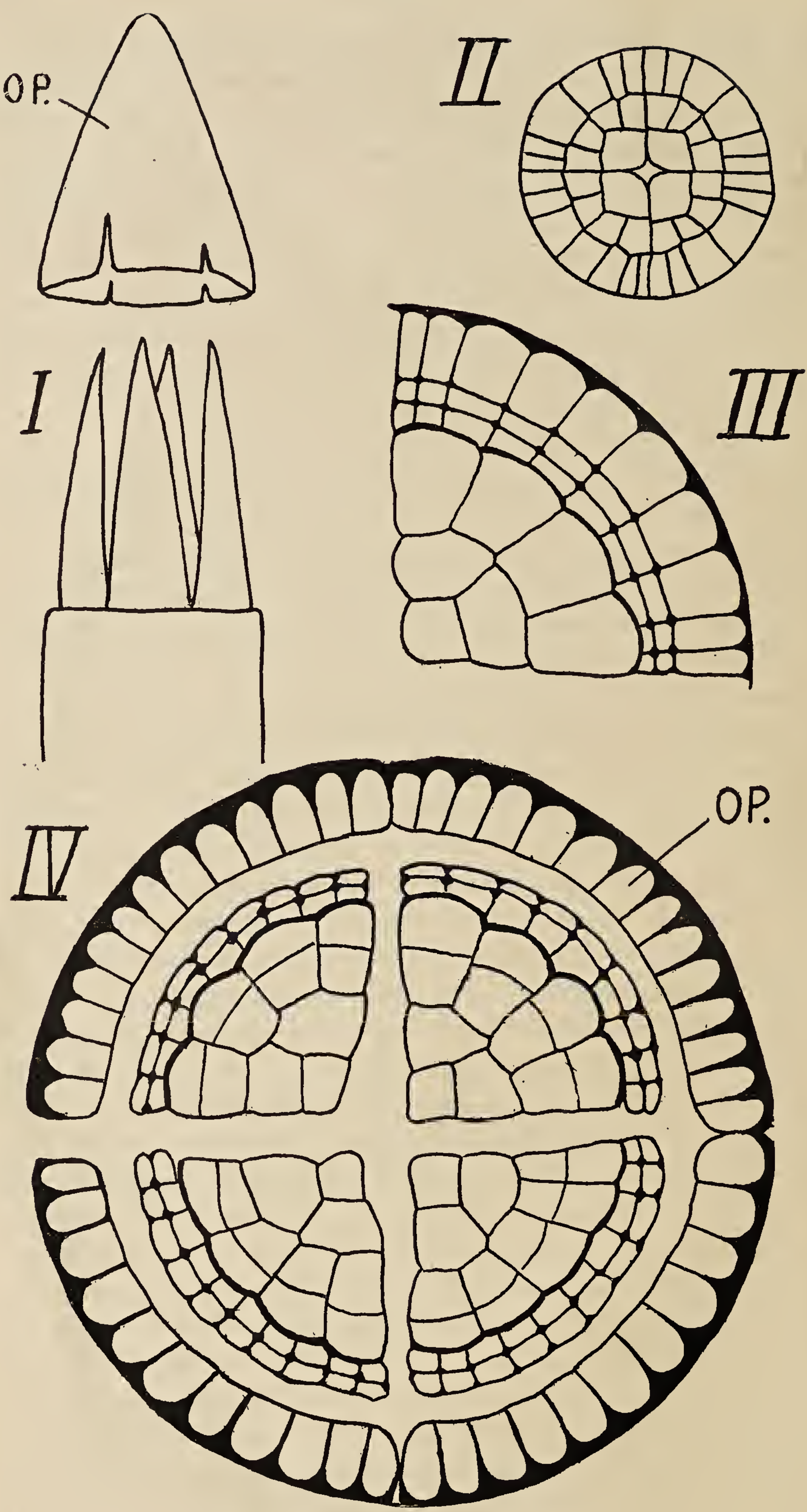


Fig. 70.—*For description see next page.*

Fig. 70.—*Tetraphis pellucida*. I. Upper portion of ripe capsule, with four peristome teeth; above is the detached operculum. II. Transverse section of young capsule, taken above the annulus; the four central cells (columella portion of the operculum) have already split apart. III. Transverse section of upper portion of nearly ripe capsule; the outermost layer of cells forms the operculum. IV. Transverse section of operculum and peristome of ripe capsule. in which the operculum has become loosened and the four teeth have split apart. II. and III. from Goebel.

(Tetraphidineæ), the Polytrichaceæ and Dawsoniaceæ as a third (Polytrichineæ), the remaining Bryales being placed in his group Eu-Bryineæ. It would seem better to raise Fleischer's sub-groups of Bryales into independent groups—Tetraphidales, Polytrichales, Buxbaumiales, and Eu-Bryales. These groups may be briefly characterised as follows:—

I. **Tetraphidales.** Peristome consists of four solid pyramidal cell-masses, formed by the splitting, along two intersecting radial planes, of the entire tissue lying within the single-layered lid (operculum) of the capsule. The group comprises two orders—Tetraphidaceæ with the genera *Tetraphis* and *Tetradontium* and Calomniaceæ with the genus *Calomnium* (with a single tropical epiphytic species). *Calomnium* has no peristome, but otherwise it closely resembles *Tetraphis*; for instance, its rhizoids, which grow on the aerial roots and stems of Ferns, produce erect branched leaf-like assimilating organs similar to those borne on the protonema of *Tetraphis*.

The peculiar and probably primitive peristome of *Tetraphis* may in some respects be compared with the elaterophore of *Aneura* and *Metzgeria* among the Jungermanniales, since the four intersecting cleavage lines appear in the apical tissue of the capsule at an early stage in development (see Fig. 70).

II. **Polytrichales.** Peristome arises in the inner zone of the amphithecium, consisting of a variable number of cell-layers, and the teeth (typically U-shaped at the base) are formed from entire cells arranged in rows or bundles. In *Dawsonia* the peristome-forming zone is broad, and the peristome consists of numerous long filaments (single cell-rows or bundles of cell-rows) which become separated by resorption of the intervening thin-walled tissue of this zone. In Polytrichaceæ the peristome arises from a single annular series of cells, in which curved dividing walls appear in such a way as to form bundles constituting a ring of thirty-two or sixty-four (rarely sixteen) short pyramidal teeth; the tips of these are joined to a thin membrane (epiphragm) formed by the basal tissue of the columella in the operculum, and a poppy-like mechanism results from resorption of the uppermost curved cells between the tips of the teeth (see Figs. 71, 72).

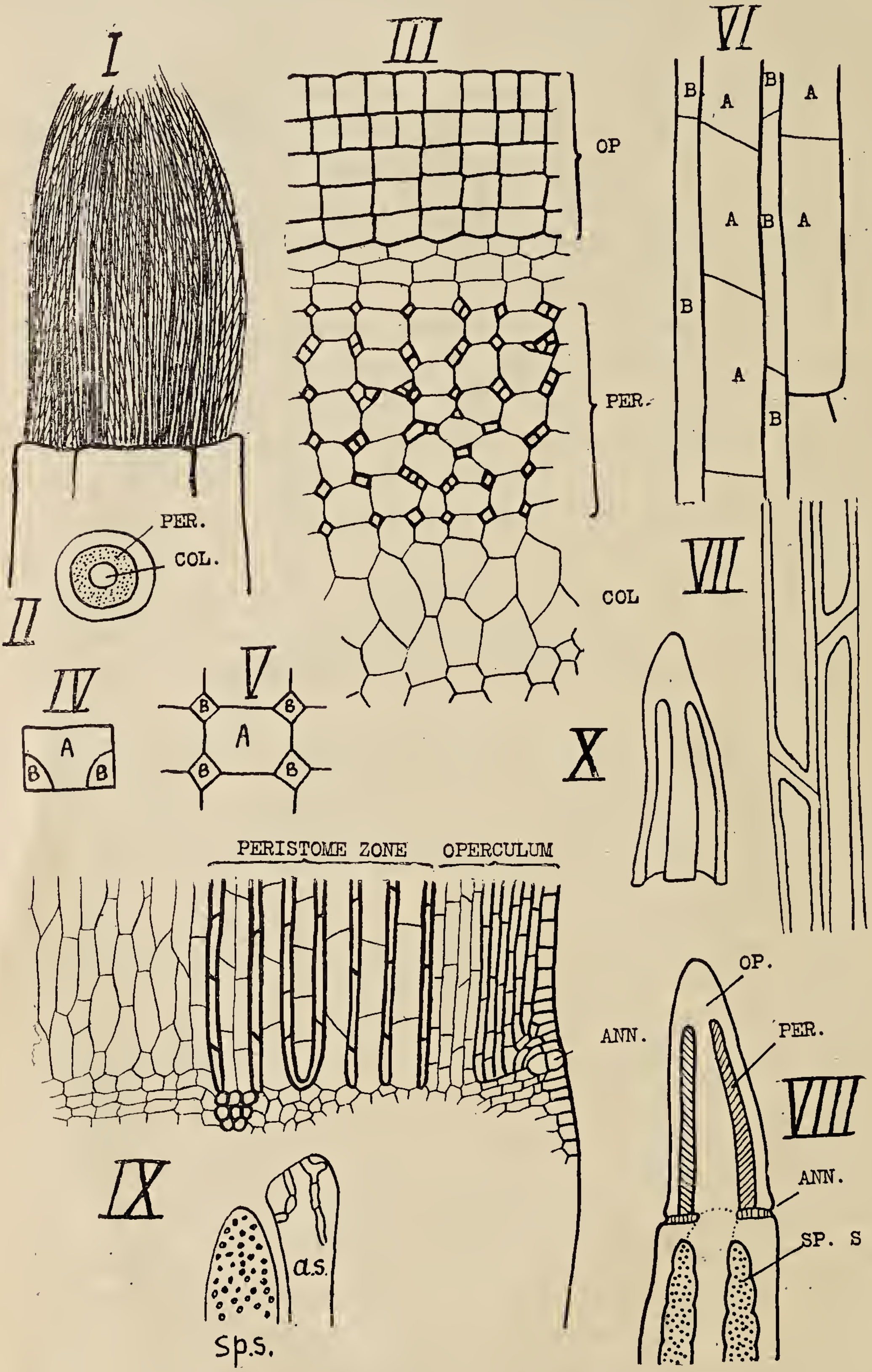


Fig. 71.—*For description see next page.*

Fig. 71.—*Dawsonia.* I. Upper portion of capsule, with peristome of numerous bristle-like processes. II. Transverse section of upper portion of young capsule, showing the relatively broad peristome-forming zone. II. A portion of III, magnified to show the narrow thick-walled cells and the wide thin-walled cells of the peristome zone—the former produce the peristome teeth, the latter break down; outside of the peristome zone is a layer of thin-walled tissue, which breaks down when the operculum becomes detached. IV and V. Diagrams showing the origin of the peristome processes (B) as small cells cut from the cells of the peristome zone, the remainder of each cell (A) being thin-walled and eventually breaking down. VI. Part of a longitudinal section of young capsule, showing the narrow peristome cells (B) and the intermingled thin-walled cells (A). VII. A portion of a peristome tooth consisting of two rows of thick-walled cells. VIII. Longitudinal section of upper portion of nearly ripe capsule. IX. A portion of VIII, magnified highly. X. Detached operculum, cut longitudinally, to show the rod-like columella tissue which comes off with the outer cone-like tissue of the cap. *A.s.*, air space; *ann.*, annulus; *col.*, columella; *op.*, operculum; *per.*, peristome; *sp. s.*, spore sac. Except I., all the figures are from Goebel, but made somewhat diagrammatic.

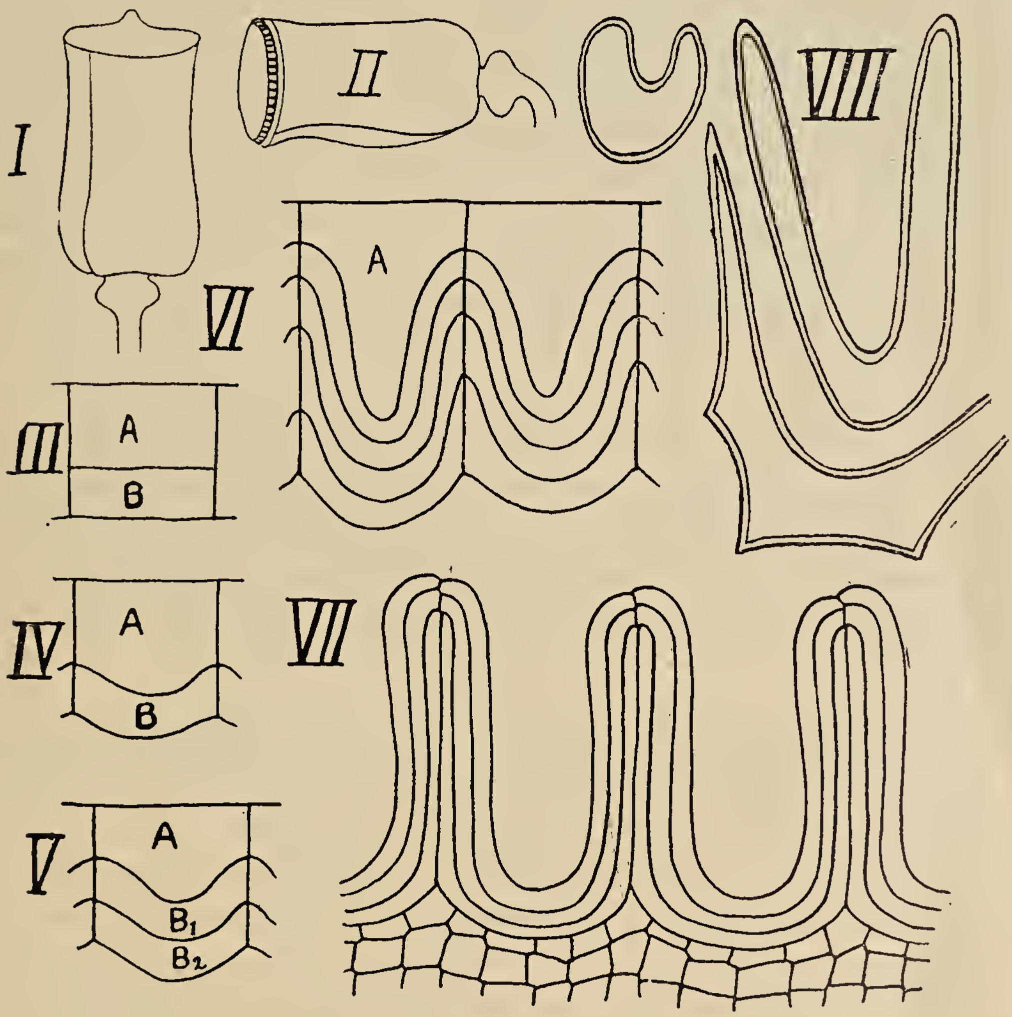


Fig. 72.—*Polytrichum.* I. Ripe capsule. II. Capsule after curvature of the seta and dehiscence of the operculum. III to VI, Diagrammatic tangential sections of the peristome-forming layer, showing the divisions which cut out the peristome-forming cells (B) from the thin-walled upper cell which becomes disorganised to form the pore between two adjacent peristome teeth. VII, three peristome teeth, each consisting of a bundle of cells. VIII, three cells isolated by maceration from a peristome tooth. III to VI and VIII from Goebel.

III. **Buxbaumiales.** Peristome double, arising in several (three to six) concentric cell layers of the amphithecium. Outer peristome (exostome) consists of from one to four series of slender teeth, the inner peristome (endostome) of a thin tubular membrane resembling a truncated cone and showing sixteen or thirty-two longitudinal folds. Both peristomes consist of thickened cell-walls only, not of entire cells, as in Tetraphidales and Polytrichales. In this respect the Buxbaumiales approach the Eu-Bryales, though the greatest distinction between the two groups lies in the fact that in Eu-Bryales the number of layers constituting the peristome-forming zone is more definitely limited.

IV. **Eu-Bryales.** Here the peristome-forming zone consists either of two or three layers of cells, the walls of which become thickened in such a way as to form typically flat triangular teeth, the unthickened walls becoming resorbed, so that the teeth consist of plates representing the thickened portions of the walls of either two or three concentric cell-layers. The horizontal walls in some cases do not undergo complete resorption, so that the teeth are then chambered and appear in longitudinal section to consist of a row of cells, though these cells are open at either side of the tooth. The number of teeth is typically either sixteen or thirty-two, more rarely eight or sixty-four. Where resorption is incomplete (e.g., *Splachnum*, *Splachnobryum*, *Leptostomum*, *Leucodon*) the peristome is regarded as being in reality double, and it is an open question whether this "chambered" type of peristome is primitive or reduced. The Eu-Bryales are sub-divided, on the peristome structure, into three series.

(A). *Haplolepideæ.* Here the peristome consists of a single series of teeth, formed of membranes belonging to two concentric cell-layers. The outer face of each tooth shows a single row of membranes, while the inner face shows two series of membranes owing to the presence of the remains of the radial walls of the inner peristome-forming layer of cells. The sixteen teeth are either simple or are divided more or less deeply into two (sometimes three) lobes or filaments. The Haplolepideæ are divided into five cohorts, differing with regard to the entire or lobed character of the teeth, the presence or absence of a collar-like "properistome" outside of the peristome, the relative thickness of the two membrane layers composing each tooth, the presence or absence of striations and papillæ on the outer and inner faces of the teeth, the presence or absence of a basal membrane to which the teeth may be joined below, etc. (i.) *Archidioideæ*, with the single genus *Archidium*. (ii.) *Dicranoideæ*. Teeth usually cleft into two or rarely three lobes, outer layer with longitudinal striations and thinner than the inner layer, which has more or less distinct transverse bars, no basal membrane, no properistome. Families:—Dicranaceæ, Fissidentaceæ, Leucobryaceæ. (iii.) *Monocranoideæ*. Teeth undivided, outer layer with papillæ, the two layers of about equal thickness, no basal membrane, properistome often present. Families:—Leucophanaceæ, Syrrhopodontaceæ, Calymperaceæ. (iv.) *Ditrichocranoideæ*. Teeth usually divided deeply into two or rarely three filamentous lobes, usually with papillæ, transverse bars feebly developed, basal membrane usually present, no properistome. Families:—Trematodontaceæ, Angstrœmiaceæ, Ditrichaceæ, Trichostomaceæ. (v.) *Platycranoideæ*. Teeth broad and thin, undivided or perforated by slits—more rarely split into two or three lobes, outer teeth thicker than inner, no basal membrane, properistome sometimes present. Families:—Seligeraceæ, Grimmiaceæ,

(B). *Heterolepideæ*. In the single small family placed here (Encalyptaceæ) the calyptra differs from that of other Bryales by its relatively large size and long-continued growth and persistence —it only becomes detached when the operculum falls off, coming away along with it. In the single genus *Encalypta*, along with great uniformity in all other characters, there is great diversity in the structure of the peristome, which may be constructed either on the Haplolepidean or the Diplolepidean plan, and in the latter case the superposed exostome and endostome are sometimes coherent, owing to incomplete resorption of the horizontal walls of the peristome-forming cells. According to Philibert, *Encalypta* represents the synthetic ancestral type from which the Haplolepideæ and the Diplolepideæ have arisen.

(C). *Diplolepideæ*. In this group there are very few cleistocarpous forms, as compared with the Haplolepideæ, and to it belong the great majority of the Bryales, including practically all the pleurocarpous forms and some of the largest of the acrocarpous families. The peristome is double, very rarely apparently single or chambered (*Splachnum*, etc.) and still more rarely absent altogether. The exostome consists of sixteen teeth, sometimes joined in pairs, occasionally perforated or split; the outer layer consists of two series of membranes, the inner of a single series. The endostome consists of very thin plates, the outer layer corresponding to the inner layer of the exostome. The thickened cell-walls that contribute to the formation of the entire peristome belong to three concentric layers of cells. As was shown by Philibert, the single peristome of the Haplolepideæ is the homologue of the inner peristome of the Diplolepideæ. It would therefore perhaps be better to apply the term "haplostome" to the simple peristome of the Haplolepideæ and to the inner peristome of the Diplolepideæ. The endostome of Diplolepideæ, however, presents much greater variety of form than does the simple peristome of Haplolepideæ; it sometimes consists of a single series of sixteen teeth, but in its typical form it is differentiated into a collar-like basal membrane (usually sharply folded or keeled), which bears on its margin a series of processes and between these a number of fine filaments or cilia. The Diplolepideæ are divided into two main series. (i.) *Epicranoideæ.* Exostome teeth superposed on the endostome processes; exostome teeth usually undivided, sometimes joined basally in pairs, sometimes joined at the tips to a small disc (e.g. *Funaria*), rarely all joined at the base to a narrow membrane; endostome not keeled, and lacking both basal membrane and cilia. The Epicranoideæ are again divided into (a) *Funariinæ* (Funariaceæ and Disceliaceæ) in which the endostome processes are free, and (b) *Splachninæ* (Splachnaceæ, Oedipodiaceæ, and Schistostegaceæ) in which the endostome is either absent or is coherent with the exostome. (ii.) *Metacranoideæ.* Exostome teeth alternating with the endostome processes; exostome teeth usually undivided, always free; endostome keeled and differentiated into basal membrane, processes, and cilia, but sometimes rudimentary and then occasionally united to the exostome, but rarely absent altogether. The Metacranoideæ, a very large group, are divided into (a) *Bryinæ* (Mitteniaceæ, Bryaceæ, Mniaceæ, Leptostomaceæ, Rhizogoniaceæ, Aulacomniaceæ, Timmiaceæ, Meeseaceæ, Bartramiaceæ, Spiridentaceæ); (b) *Isobryinæ* (Drepanophyllaceæ, Eustichiaceæ, Orthotrichaceæ, Erpodiaceæ, Cryphæaceæ, Leucodontaceæ, Pterobryaceæ, Fontinalaceæ, Climaciaceæ, Hedwigiaceæ, Meteoriaceæ, Sorapillaceæ, Neckeraceæ, etc.); (c) *Hookerinæ* (Nemataceæ, Pilotrichaceæ, Hookeriaceæ, Hypopterygiaceæ); (d) *Hypnobryinæ* (Fabroniaceæ, Entodontaceæ, Hypnaceæ, Brachytheciaceæ, etc.). These sub-divisions are based partly on minor characters of the peristome, partly on vegetative characters of the gametophyte.

IX. INTER-RELATIONSHIPS OF THE HIGHER BRYOPHYTA (SPHAGNALES, ANDREÆALES, TETRAPHIDALES, POLYTRICHALES, BUXBAUMIALES, EU-BRYALES).

IN seeking for a starting-point for the evolution of the higher Bryophytes, or Mosses, one is struck by the remarkable resemblances between the Sphagnales on the one hand and the Anthocerotales and (to a smaller extent) the Jungermanniales on the other. Apart from the flat thalloid protonema, which suggests comparisons with both the lower Jungermanniales and the Anthocerotales, *Sphagnum* resembles the former group in the structure and dehiscence of its antheridium, and in the early development of the sporophyte. However, apart from the fact that in *Sphagnum* the young antheridium grows by an apical cell, instead of showing the intercalary growth characteristic of the Liverworts, it may be noted that in *Buxbaumia* the antheridium is very similar to that of *Sphagnum*. *Buxbaumia* is in many respects primitive, and it is interesting to note that in this genus the young leaf, instead of growing by an apical cell as in other Mosses, shows the bilobed condition characteristic of the Acrogynæ. It would appear that in *Sphagnum* the sexual organs and the leaves have departed from the intercalary mode of growth found in Liverworts, and show the apical cell growth found in the higher Mosses, but the sporogonium still undergoes intercalary growth and in its earliest stages presents a close resemblance to the embryo of Jungermanniales. The striking similarity between *Sphagnum* and the Anthocerotales in the origin and form of the archesporium suggests that *Sphagnum* has probably arisen from a synthetic ancestral type which combined

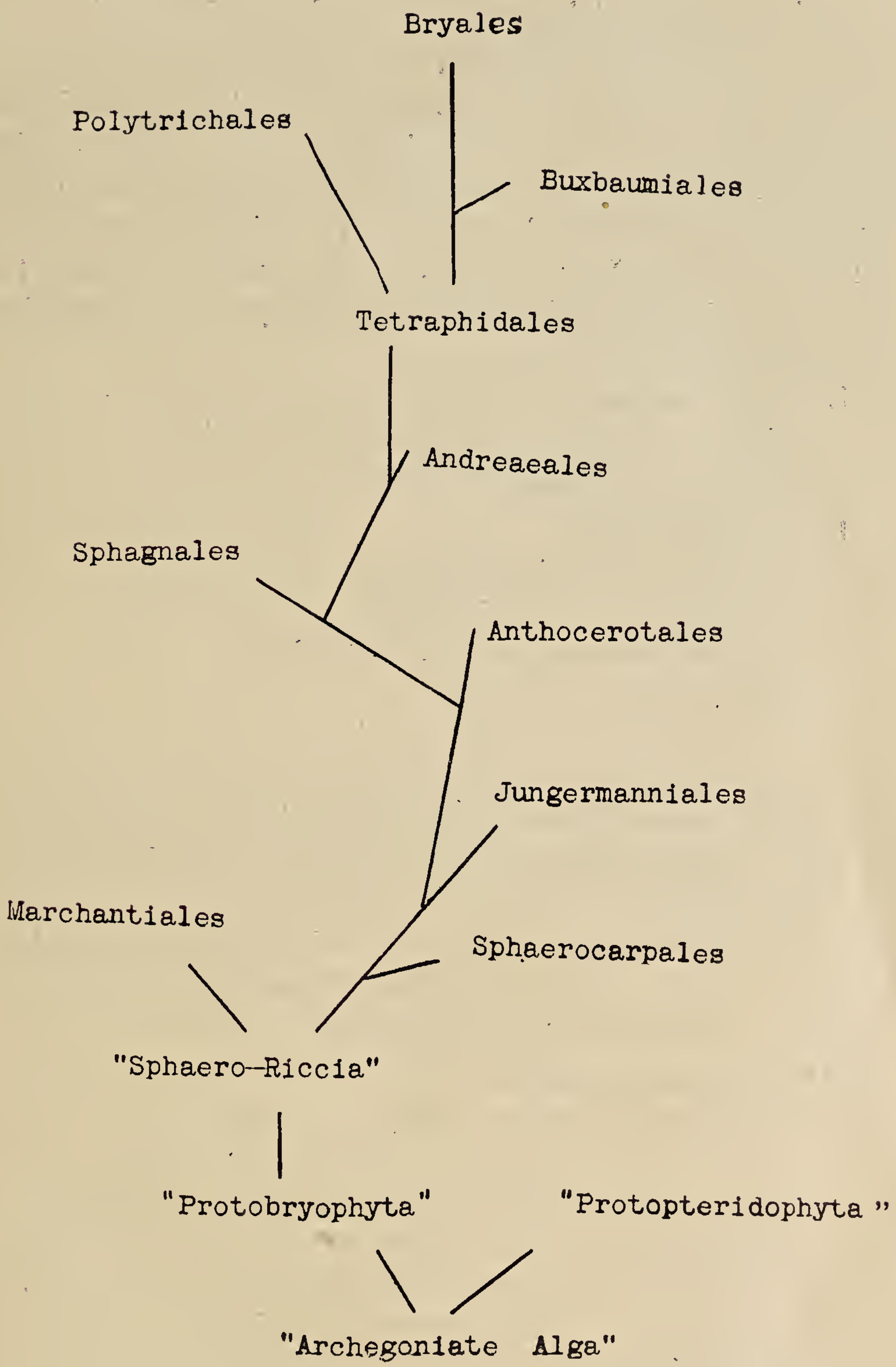
Jungermannian and Anthocerotean characters, and since the Anthocerotales diverge considerably from the other Liverworts, at any rate in the development and structure of the sporogonium, we might assume that the hypothetical primitive "Sphæro-riccia" type gave rise on one hand to the Sphærocarpales, Marchantiales, and Jungermanniales, and on the other to the Anthocerotales and Sphagnales. It must be admitted, however, that the gap between the Sphagnales and the Anthocerotales is much wider than that between the Anthocerotales and the other Liverworts. The four groups of lower Bryophytes (Sphærocarpales, Marchantiales Jungermanniales, Anthocerotales) agree with each other, and differ from the higher Bryophytes, in the development of the sexual organs by means of intercalary growth and not by an apical cell, in having unicellular rhizoids, in the absence of an apical cell from the leaves in the case of foliose forms, and in the presence (except in Ricciaceæ) of sterile cells (typically developed as elaters) in the archesporium.

In the Bryales, the most striking advance upon the lower groups is the evolution of the peristome. If we assume that some at least of the cleistocarpous Bryales are primitive, it would be easy to trace from types like *Archidium* and *Phascum* a series of lines leading up to the typical Bryales, and this possibility should not be lost sight of. There has been a general tendency to regard these cleistocarpous genera as reduced, but in the writer's opinion the question of their position and affinities is quite as open as in the case of the Ricciaceæ. However, setting aside these doubtful forms, the genus *Andreæa* appears to point to a possible connecting-link between Sphagnales and Bryales, and also to throw some light upon the origin of the peristome. In *Andreæa*, the archesporium, though arising in the outermost zone of the endothecium, is completed above—just as in *Sphagnum* and Anthocerotales—by a zone of tissue extending across the entire endothecium, so that the columella is incomplete and is covered above by the dome-like archesporium.

In the writer's view, there appears to be a definite correlation between the form of the archesporium and the fate of the apical tissue of the capsule. When the archesporium is dome-shaped, the sterile apical tissue is practically cut off from the stream of food materials brought upwards from the gametophyte, through the conducting-strand of the seta and thence through the columella of the capsule, and these materials are almost entirely used up in the nutrition of the developing spores. This suggestion appears to be supported by a variety of facts in the morphology of the capsule in the lower Bryophytes. In these plants (Sphærocarpales, Marchantiales, Jungermanniales) the archesporium is a cell-mass derived from the entire endothecium, and in the great majority of cases sterilisation is confined to the formation of elaters, the amphithecium giving rise to the capsule-wall; but sometimes an imperfect columella of sterile tissue is formed (e.g., *Pellia*, *Aneura*) and there is some evidence that the endothecium may contribute to the formation of a lens-like cap or apical thickening of the capsule-wall (e.g., *Reboulia* and some other Marchantiales). In these lower Bryophytes, the elaters serve to nourish the developing spores, and after becoming thickened and losing their original contents they act as conductors of water and dissolved salts, finally assisting in spore dispersal at dehiscence of the capsule. As sterilisation became more definitely localised and complete in the central region of the capsule tissue, the elaters would become less important for the nutrition of the developing spores, and in the higher Bryophytes they have disappeared altogether. The absence of elaters in the Mosses may be correlated with the provision of dehiscence mechanisms which ensure the gradual dispersal of the spores through relatively small apertures. In most of the non-operculate (cleistocarpous) Bryales, the capsule is sessile or has a very short seta, and is shorter than the leaves which surround it, hence when the spores are set free by irregular rupture or decay of the capsule-wall they do not fall in a mass to the soil, the leaves acting functionally like a peristome and forming narrow spaces through which the spores may be gradually dispersed by wind or rain; in most of these forms the spores are relatively large and few. In some cleistocarpous Bryales, however, there is a well-developed seta (e.g., *Phascum*) which may attain a considerable length (e.g., *Voitia*), and in these forms the spores are usually much smaller than in cleistocarpous species with sessile or almost sessile capsule; in *Phascum*, etc., the capsule becomes detached from the seta, leaving a basal aperture through which the spores escape gradually when the capsule falls away, while in *Voitia* the entire sporogonium becomes detached, and the spores apparently escape (after rupture or decay of the capsule-wall) through a slit in the relatively large and persistent calyptra. A similar condition occurs in *Calymperes*, in which the persistent calyptra opens by several longitudinal slits. In all cases, there is a mechanism of some kind for gradual spore dispersal, and this attains its highest development in the typical double peristome of the Diplolepideæ, the dominant Moss group and the culminating point of Bryophyte evolution. Comparison of a large number of Bryales shows that in general there is a definite relation between the size of the spores and the diameter of the apertures between the endostome processes and cilia—the smaller the spores the more numerous and completely developed are the cilia of the endostome.

In the higher Mosses, the tubular or barrel-like form of the archesporium, which is open above and below, allows ready passage of food materials to the apical region of the capsule, and in this region considerable growth occurs, leading to the development of annulus, operculum, and peristome. We may perhaps assume that the *Tetraphis* type of peristome is the most primitive, and that it is derived from that seen in those species of *Andreæa* in which the slits in the capsule-wall extend to the apex of the capsule and thus lead to the formation of a series of teeth. In Tetraphidaceæ the entire tissue of the capsule apex takes part in the formation of the simple peristome, the epidermal layer itself separating from the underlying tissue to form an operculum only after it has become slit into four lobes at the base. In the Polytrichales, we find that the development of the peristome is confined to a zone of amphithecial cells surrounding the columella; in the more primitive *Dawsonia* type this zone is several cells deep, while in the more advanced *Polytrichum* type it is limited to a single layer of cells. In the *Buxbaumia* type, again, the peristome-forming zone is broad, and the number of teeth forming the exostome is indefinite, these teeth being arranged in several concentric series. Finally, in the Eu-Bryales the peristome arises in a sharply defined zone of amphithecial cells and the teeth are always in two series. Along with this limitation of the peristome-forming zone to fewer and fewer layers of cells, we find a transition from the primitive *Tetraphis* type in which the peristome teeth consist of cell-masses to the *Bryum* type in which it consists solely of the remains of thickened and persistent cell-membranes.

The phylogenetic views thus briefly and tentatively put forward may be expressed diagrammatically in the accompanying table.



Phylogeny of the Bryophyta.

X. CLASSIFICATION OF THE BRYOPHYTA.

Since various modifications in the generally accepted classification of the Bryophyta have been suggested and discussed in the preceding pages, it will be convenient to set out here a table showing the proposed divisions of this phylum, with an enumeration (except in the case of the Eu-Bryales) of the families included in each of the ten divisions (Orders). The characters of these ten divisions have been given in some detail already, and are therefore not repeated here.

I. **Sphærocarpales.**

Sphærocarpaceæ.—*Sphærocarpus, Geothallus.*
Riellaceæ.—*Riella.*

II. **Marchantiales.**

Ricciaceæ.—*Riccia, Tesselina.*
Corsiniaceæ.—*Corsinia, Boschia.*
Targioniaceæ.—*Targionia, Cyathodium.*
Monocleaceæ.—*Monoclea.*
Cleveaceæ (Astroporeæ).—*Clevea, Santeria, Peltolepis, Gollaniella.*
Aytoniaceæ (Operculatæ).—*Plagiochasma, Reboulia, Neesiella, Cryptomitrium, Grimaldia, Massalongoa, Fimbriaria.*
Marchantiaceæ (Compositæ).—*Exormotheca, Fegatella, Wiesnerella, Dumortiera, Monoselenium, Lunularia, Preissia, Bucegia, Marchantia.*

III. **Jungermanniales.**

Aneuraceæ.—*Aneura, Metzgeria, Podomitrium, Umbraculum.*
Blyttiaceæ.—*Blyttia, Mörckia, Symphyogyna, Makinoa.*
Codoniaceæ.—*Pellia, Calycularia, Blasia, Cavicularia, Noteroclada, Petalophyllum, Fossombronia, Treubia.*
Calobryaceæ.—*Calobryum, Haplomitrium.*
Lophoziaceæ.
Cephaloziaceæ.
Ptilidiaceæ.
Scapaniaceæ.
Radulaceæ.

Pleuroziaceæ.
Porellaceæ.
Lejeuneaceæ.

IV. **Anthocerotales.**
Anthocerotaceæ.—*Anthoceros, Notothylas, Megaceros, Dendroceros.*

V. **Sphagnales.**
Sphagnaceæ.—*Sphagnum.*

VI. **Andreæales.**
Andreæaceæ.—*Andreæa.*

VI. **Tetraphidales.**
Tetraphidaceæ.—*Tetraphis, Tetradontium, Calomnium.*

VIII. **Polytrichales.**
Dawsoniaceæ.—*Dawsonia.*
Polytrichaceæ.—*Polytrichum, Catharinea, Lyellia,* etc.

IX. **Buxbaumiales.**
Buxbaumiaceæ.—*Buxbaumia.*
Diphysciaceæ.—*Diphyscium.*

X. **Eu-Bryales.**

The old-established primary division of the Bryophyta into the two classes Hepaticæ (including the first four of the Orders enumerated above) and Musci has only been called in question in connexion with the two groups Anthocerotales and Sphagnales. It is of interest to note that in certain of the characters which have been used to exclude the Anthocerotales from the Hepaticæ on one hand, and the Sphagnales from the Musci on the other, these two aberrant groups show a striking resemblance to each other. If the Anthocerotales are to be made a separate class apart from the Hepaticæ, either Sphagnales should also be considered a separate class apart from the Musci, thus making four primary divisions of Bryophyta—Hepaticæ proper, Anthocerotes, Sphagna, and Musci proper—or the Anthocerotales and Sphagnales might he united to form a class intermediate between the "Eu-Hepaticæ" and the "Eu-Musci," thus giving three classes of Bryophyta. The most striking character which is common to Anthocerotales and Sphagnales, as compared with the remaining Bryophyta, is the origin of the archesporium as a dome-like layer formed chiefly from the amphithecium and completed above across the endothecium, the columella—covered by the archesporium—being derived from the endothecium. On the other hand, however, Anthocerotales and Sphagnales are separated by differences in the development of the sexual organs, and it would appear that these differences are absolutely characteristic of the two generally recognised divisions of Bryophyta. In all Hepaticæ that have been investigated, both the antheridium and the archegonium show intercalary growth, while in all Musci the young sexual organs grow by means of an apical cell. This generalisation has been challenged by Gayet, who claims that in all the groups of Bryophyta, excepting Anthocerotales, an active apical cell is present which produces the neck-cells but not the canal-cells, the latter being formed from the same mother-cell as that which gives rise to the oosphere and ventral canal-cell. According to Gayet, *Anthoceros* is the only Bryophyte in which the entire growth of the archegonium is intercalary. Campbell has pointed out that Gayet's methods are quite inadequate for the purpose of deciding this somewhat difficult question, and the results of the comparatively few recent researches in which the development of the archegonium has been carefully followed have shown that in Hepaticæ (including Anthocerotales) the archegonium does not at any stage grow by means of an apical cell, while in Mosses (including *Sphagnum*) an apical cell is present, its segments giving rise to the entire neck and its canal-cells.

In the writer's opinion, if any departure at all is to be made from the customary classification of the Bryophyta into Hepaticæ and Musci, it would be better to divide the whole phylum into the ten independent groups enumerated above, without setting the Anthocerotales and the Sphagnales apart from the remaining Hepaticæ on one hand and the remaining Musci on the other.

LITERATURE OF TETRAPHIDALES, POLYTRICHALES, BUXBAUMIALES, AND EU-BRYALES.

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ON INHERITANCE OF A MUTATION IN THE COMMON FOXGLOVE *(DIGITALIS PURPUREA)*.

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[Plate I and Text-Figs. 1-12.]

THE common Foxglove is well known for its frequent habit of sporting, and references to various monstrous forms abound in teratological literature. Most of these abnormalities come under the head of fasciation, proliferation, synanthy or peloria. In the present case the modification is of quite a different character and is confined to the corolla, the members of which are more or less completely disjoined (dialysis), some or all of the petals being furthermore converted into stamens (staminody). The result is a flower which is hardly recognisable as a foxglove at all. This curious form, though less commonly met with than the peloric variety, has been known for a considerable time. Penzig[1] speaks of it in conjunction with syanthy and peloria as a "classic" monstrosity; as early as 1826 it was figured and described by de Chamisso,[2] who names it *D. purpurea heptandra*. Later, in 1882, a specimen which had been gathered at Tilburstow Hill, Surrey, and sent to him, was described and figured by Henslow.[3] Analogy with the case of peloria would lead us to suppose that the peculiar modifications characteristic of the *heptandra* form might also be found to be inherited. This expectation finds a certain confirmation in various scattered references recording the reappearance of this form from time to time. De Chamisso,[4] it is true, states in a later note that none of the three plants which he obtained from the *heptandra* parent showed any trace of the peculiarity, but as the *heptandra* parent was not apparently isolated, this observation can hardly be used as evidence on this point. On the other hand a writer in "The Gardeners' Chronicle" states that a seedling foxglove exhibiting staminody of three of the petals was derived from a parent similarly deformed.[5] In another instance seedlings from a specimen observed by Mr. Smith of Daisy Hill Nursery, Newry, are stated all

[1] Pflanzen-Teratologie 2, p. 210.

[2] *De Digitali purpurea heptandra.* Linnæa I, p. 371, Tab. VI.

[3] Journ. Linnean Soc., XIX, Botany, pp. 216-218, 1882.

[4] Linnæa IV, p. 77.

[5] G. C., 1874. 2, p. 78.

to have reproduced the deformity.[1] The number of plants raised is not, however, stated. Again recently, while this account was already in progress, a specimen was exhibited at a meeting of the Linnean Society by Professor Dendy, on behalf of Dr. N. C. Macnamara.[2] The spike in question had, according to the account, been cut from a plant grown from seed of a sport that had appeared in 1907, and showed the extreme form in which the five divisions of the corolla are represented by five stamens. Here too it was observed that the peculiarity came true from seed. In none of these cases, however, have we full information regarding the statistical evidence on which the general statement as to inheritance is based, nor have I been able to find any account of observations continued beyond the first generation. The following experiments were therefore undertaken with a view to ascertaining to what extent this form breeds strictly true, and the nature of its relation to the type. From the results which follow it will be seen *that offspring of* heptandra *parents all show dialysis and staminody of the corolla, but the extent to which these malformations are exhibited varies not only in different individuals, but in different flowers on the same individual*; *further, that the* heptandra *form is related to the type as recessive to dominant.*

A specimen of *D. purpurea*, exhibiting the peculiarities above described was shown to me in 1906 by a friend, in whose garden in Cambridge it had appeared among a number of normal plants which had been grown from a single packet of seed.[3] It was then already late in the season, and none of the flowers which were artificially fertilised set seed. A considerable number of good capsules were, however, gathered from the flowers which had been exposed and naturally fertilised. From seed thus obtained a first generation of plants were flowered in 1908, and a second in 1910. The following account contains the results of observations made during these two seasons.

I.—Description of *D. purpurea heptandra.*

All individuals showing the general features previously mentioned, *viz.*, dialysis and staminody of the corolla, are included under this title.

In *heptandra*, as in the type form, the axillary buds at the lower nodes develop in most cases into short shoots bearing a few leaves below the flowers. At the succeeding nodes, as a rule though not universally, the shoot is replaced by a single flower bud which does not reach full development. Some of these buds remain quite rudimentary, others develop further and may produce functional organs; but even in this latter case growth ceases while the parts are still enclosed in the calyx. Afterwards follow the fully developed flowers which continue to near the top of the spike, where they may again be replaced by buds which never unfold. It may happen, however, that no buds are arrested at the base of the spike, in which case the full-sized flowers follow immediately upon the leafy shoots.

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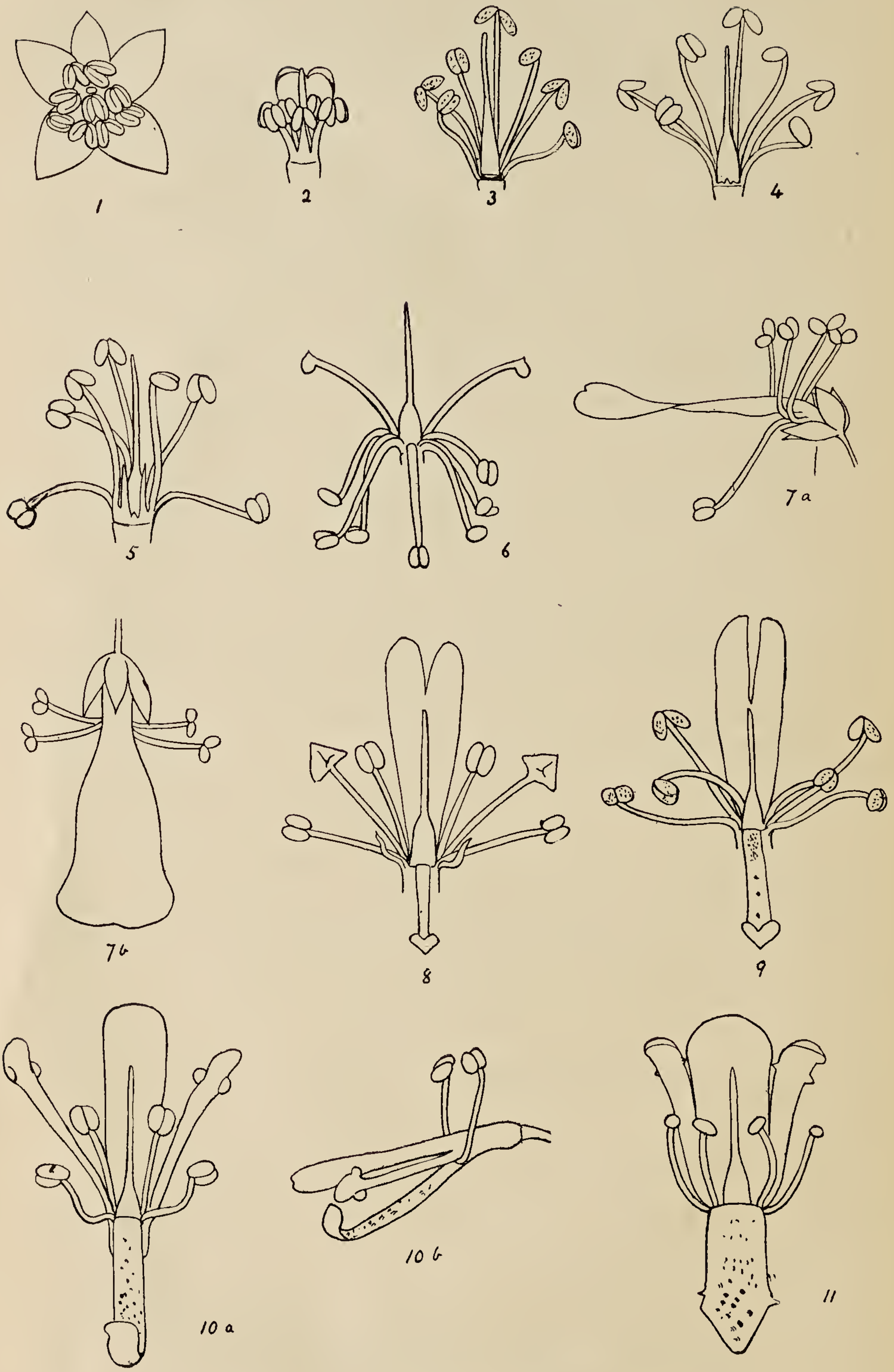
[1] Ibid., 1904, 2, p. 208.

[2] See Proceedings of the Linnean Society for 1910, p. 106.

[3] Most observers have, as in this case, recorded only a single sport in the first instance, though Henslow's case appears to have been an exception.

Only a few of the *heptandra* individuals exhibit a complete absence of petal-like structures *throughout the whole of the inflorescence*; though now and again an individual will be found to show this condition from top to bottom of the spike. In these cases the *apparently* total absence of corolla gives the spike a very curious, albeit, quite uniform appearance. In the great majority of the plants, however, it is noticeable that in travelling up the spike the flowers present a graduated series; dialysis and staminody of the corolla gradually diminish, and reversion may even be carried so far that eventually normal flowers are produced near, or at the top of the inflorescence. This increasing tendency towards normality may extend to the summit of the spike, or it may reach high-water mark below, but so near the apex, that whatever stage in the progressive series is reached at this point is maintained upwards to the top. In other cases the wave may spend itself some distance below the summit, and the later flowers then form a downgrade series ending in partial, or occasionally, if arrested flowers occur in this region, in complete return to the extreme *heptandra* condition

The choice of the name *heptandra*, as it proves, is not altogether happy, for although it correctly describes the condition occurring in the great majority of the flowers (*i.e.*, those having the three petals of the lower lip replaced by three stamens more or less similar to those of the andrœcium proper, thus making seven stamens in all), it is not strictly applicable in those cases where a greater or lesser degree of deviation from the normal occurs. Thus, on the one hand, almost every stage may be found between the true heptandrous condition and the normal flower with four stamens; while at the other end of the scale we meet with the extreme case in which both lips of the corolla are replaced by stamens, so that nine (or rarely ten) stamens are present, and the flower appears to lack all five



Text-figs. 1—11.

petals.[1] Several intermediate forms occur, and the various modifications which form a progressive series will be most easily exhibited in the accompanying table.

Modifications of the Corolla.

(*a*). *Upper lip.*

1. The upper lip may be wholly wanting. The posterior part of the tube is then reduced to a mere rim with an even concave outline (see fig. 3).

The upper lip may be represented by:—

2. Two projections on the posterior rim of the tube (see fig. 4).

3. Two filaments presenting all stages between 2 and 4 (see fig. 5).

4. Two filaments equal in length to those of the ordinary stamens, and bearing a one-lobed anther which forms normal pollen and dehisces when ripe (see fig. 6).

5. Two stamens bearing bilobed anthers similar to those of the ordinary stamens. (Only observed in very few cases). (See fig. 1).

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[1] This extreme stage does not appear to have been present in de Chamisso's plant.

Text-figs. 1—11, shewing various forms of *heptandra* flowers seen in different views. All the figures are taken from full-sized flowers, except figs. 1 and 2.

1. Arrested flower seen from above with calyx and nine stamens.

2. Arrested flower seen from the side showing an upper lip of two small petals and seven stamens. Calyx removed.

3. Flower seen from the back showing seven stamens. The lower lip of the corolla is represented by three stamens, distinguished from the andrœcium proper by the divergent anther lobes; upper lip wholly suppressed, the posterior side of the flower tube being reduced to a mere rim with an unbroken concave outline. Calyx removed. The speckled anthers show that if the corolla had been normal, the spots would have been coloured red.

4. Flower showing three small projections on the posterior rim of the flower-tube which probably represent the rudiments of the upper lip, and the posterior stamen; otherwise as fig. 5.

5. Flower showing a rudimentary upper lip in the form of two filaments; otherwise as fig. 6.

6. Flower in which the upper lip is represented by two stamens, each bearing a half anther. Calyx removed. Seen from the front.

7. Flower with upper lip of two completely fused petals. (*a*). Seen from the side. (*b*). Seen from above.

8. Flower with upper lip of two partly fused petals. The three structures representing the lower lip still bear anthers, but they are gradually becoming petaloid. Two outgrowths—the *lacinulæ corollinæ* of de Chamisso—are seen on either side. Calyx removed. Seen from the front.

9. Flower showing an upper lip of two partly fused petals. The central one of the three structures representing the lower lip has become more distinctly petaloid. Calyx removed. Seen from the front.

10. Later stage in reversion. (*a*). Seen from the front. (*b*). Seen from the side. The speckling on the anthers has been omitted here and in fig. 11.

11. Later stage still. Seen from the front.

6. Two small flattened structures, more or less coherent, in shape like miniature petals, but green, and remaining enclosed within the calyx. (Chiefly found in the arrested flowers). (See fig. 2).

7. Two large petal-like structures, either only partly coherent and appearing like narrower or broader strips of a normal corolla, or completely fused (see figs. 7-10).

(*b*). *Lower lip.*

The lower lip may be present as :—

1. Three stamens with normal anthers resembling those of the andrœcium proper, or with the lobes slightly divergent (see figs. 1-6).

2. Three stamens with very divergent lobes to the anthers. The anthers thus become sagittate in form, whereas those of the andrœcium proper are oval (see figs. 8, 9).

3. Two lateral stamens with broad flattened filaments, and an anterior structure which becomes increasingly petaloid, with an anther lobe on either margin. As the petal-like form of all three structures becomes more pronounced the anther lobes gradually disappear (see figs. 10, 11).

4. A single petaloid structure of three coherent petals which shows progressive stages of fusion with the upper lip until a normal corolla results.

Modifications of the Andrœcium.

1. The posterior stamen may be present bearing a normal anther. Such cases occur rarely among the arrested flowers, and the ten stamens are then so arranged that the flower becomes almost actinomorphic.

2. A small, often coloured, projection may arise from the rim of the flower-tube in the position of the posterior stamen, which may represent a stage in the suppression of this structure (see fig. 6).

3. The filaments of two adjacent stamens may fuse so that the resulting single structure bears a double anther.

In addition to the anther-bearing structures representing the corolla, described above, linear outgrowths of the tube—the "*lacinulæ corollinæ*" of de Chamisso—are often to be found in those flowers exhibiting the more extreme degrees of staminody (see fig. 8).

In all the *heptandra* forms the members of the corolla and andrœcium unite at the base to form a short tube region, so that these parts still become detached as a whole just as in the type. In the more extreme cases the stamens, instead of being grouped

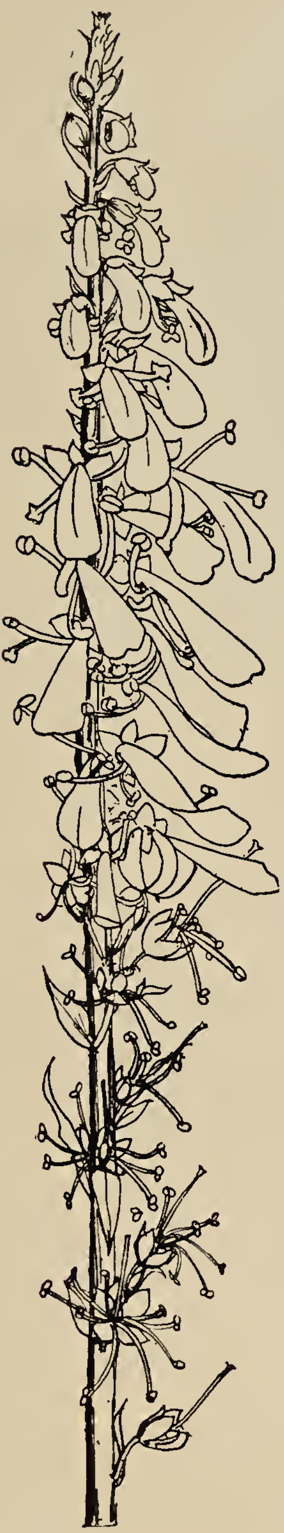

Fig. 12. A characteristic spike of the *heptandra* form proper. In the lower flowers the corolla *appears* to be wholly wanting. In those above staminody of the lower lip still persists, but the upper lip develops as a flattened petaloid structure. The stamens, unrestrained by a corolla-tube, are seen diverging in different directions.

together and curving forwards, diverge in a horizontal and backward direction, owing no doubt to the absence of the restraining force exerted, in the case of the type form, by the enclosing tube of the corolla. At the same time the ovary and style are directed upwards, this again is no doubt due to the absence of a corolla tube. As a result of this upward inclination of the style, the ring of stamens, although becoming detached when the flower is over, remains *in situ* long after it is withered, threaded as it were by the style; thus a spike which has finished flowering may still be covered through-out its length with these withered remains. In the more petaloid intermediate forms the weight of the detached portion of the flower is sufficient to bend down the style, and the whole structure slides off before withering as in the type form.

Bees are able to work all the various *heptandra* forms, and in fact seem to visit type and variety indiscriminately. But though a good quantity of seed is usually obtained from exposed *heptandra* plants, the yield from covered individuals is always scanty, and in a wet season may be almost *nil*, for both pollen and stigma are fully exposed to rain, and the rotting of the deciduous parts *in situ* favors the growth of mould.

II.—RESULTS OF BREEDING EXPERIMENTS.

From the results obtained it appears that *D. purpurea heptandra* breeds true in that from *heptandra* individuals only *heptandra* forms have been obtained. As stated above, however, the extent to which the characteristic features of dialysis and staminody are exhibited by any individual is not generally constant throughout the flowering period, but varies in the different flowers according to their position (level) on the spikes (fig. 12). As a rule the flowers in order on an axis form a graduated series, but the particular grade with which the series begins and ends, and the number of grades exhibited vary in different individuals. Further, the series may be either wholly up-grade, approximating more and more to the normal as we approach the top of the spike, or the culminating point in the reversionary series may be reached below the apex, and may be followed by a series of down-grade stages. We have as yet no very definite knowledge of the forces regulating this wave-like tendency, but it can hardly be doubted that it is not assignable to any single cause, but is due to the combined action of a number of factors, of which some exert a preponderating influence at one time, some at another, with the result that the balance is inclined at first towards, and later, perhaps, away from the condition of normality. We can thus understand how it is that the phase exhibited by the open flowers on a lateral branch may not correspond with that of those opening simultaneously on the main axis; or again that the condition of fasciation is often accompanied by a sudden break in the regularity of the series. It is not surprising that the state of vigour of a lateral branch beginning to flower should be different from that of the main axis which is already probably well advanced in its flowering period; hence on the lateral branch the first flowers may start from a point in the series behind that already reached by the open flowers on the main axis, but yet not so far back as to recapitulate the whole series. In the case of fasciation, flowers borne at the level where fasciation begins to occur may show a sudden jump as regards increased size of the petaloid structures, as compared with the flowers borne immediately below the fasciated region, or with those opening simultaneously on a normal stem of the same individual. The *heptandra* individuals are, however, easily sorted from the type plants notwithstanding this grading, for in most cases the distinction between variety and type is absolute, all the flowers on the spike being deformed in some degree in the one case, and normal in the other. Even when this is not the case there is still a very wide gap between the heptandrous individual which eventually produces a small number of normal flowers and the type plant which shows a trace of the abnormality in some of the earliest flowers. No true intermediates were observed in any of the matings. If they occur, they are evidently rare. Within the *heptandra* class we may conveniently group the several grades as follows:—

1. Extreme *heptandra* form. Plants in which all, or almost all, the flowers are without petal-like structures.
2. *Heptandra* form proper (fig. 12). Plants in which only the flowers in the lower region of the spike and those at the extreme top appear to have no corolla. In the intervening region the upper lip appears as a conspicuous petaloid structure which is usually deeply bifid. By far the larger number of *heptandra* plants belong to this group.
3. Intermediate *heptandra* form. Plants in which all, or nearly all, the flowers are more or less petaloid. The lowest flowers, in which an upper lip is often already well-developed, are succeeded by others in which a lower lip also gradually makes its appearance, and finally tubular or even quite normal flowers may be found towards the top.

As previously stated the only seed obtained in 1906 was collected from exposed flowers on a single individual. It was therefore to be expected that much of this seed would have resulted from crossing with neighbouring type plants, but that some would be due to self-fertilisation. Some 240 plants raised from this seed were flowered in 1908 of which more than 100 showed the *heptandra* characters, while the remainder resembled the type. In this case the precise numbers have no value as the fertilisation of the seed-parent was not controlled, but from the appearance of so many *heptandra* offspring it was scarcely doubtful that, when self-fertilised, this form would be found to breed true; the results in 1910 have shown that such is the case. Six of the *heptandra* individuals flowering in 1908 were self-fertilised and all the 256 offspring were *heptandra*.[1] The numbers obtained in each case were as follows:—

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[1] A single type plant was found in the rows, but that this was a rogue was evident from the fact that it possessed the smooth stem occurring in certain other families, but not otherwise found in the six families above mentioned, the 256 individuals composing them all showing the normal degree of hoariness (see p. 60).

Form of Union.	Reference Number of Family.	Number of Offspring obtained in the 2nd generation.	
		Heptandra.	Type.
Heptandra × Self	1	88	*Nil.*
	2	47	,,
	3	50	,,
	4	44	,,
	5	7	,,
	6	20	,,
	Total	256	*Nil.*

Families 1, 4, 5, and 6 were derived from plants of the *heptandra* form proper, the total offspring of 159 included :—

8 extreme *heptandra* form (*i.e.*, with all, or nearly all, the flowers non-petaloid).
143 *heptandra* form proper (*i.e.*, with a large number of flowers having a petaloid upper lip).
1 intermediate *heptandra* form (*i.e.*, with some flowers having both the upper and the under lip petaloid).
7 particular form not recorded.
——
159

In the one intermediate *heptandra* plant recorded in this group of families normal flowers were not produced. The furthest point reached in the reversionary series was that in which the lower lip was deeply lobed, and only united for a short distance with the upper lip to form a tube.

Families 2 and 3 were derived from plants of the intermediate *heptandra* form ; the total offspring of 97 included :—

7 extreme *heptandra* form,
36 *heptandra* form proper,
49 intermediate *heptandra*,
5 particular form not recorded,
—
97
—

About two-thirds of the intermediate *heptandra* plants eventually produced some normal flowers.

From the facts given above it is evident that the *heptandra* character is inherited, and that from *heptandra* parents only *heptandra* offspring are obtained. Further observation, however, is required to determine how far the degree of heptandry exhibited by the parent is reproduced in the offspring. So far as it goes, however, the evidence indicates that the offspring of a plant with a range from a moderate to a high degree of reversion will exhibit, on the whole, a greater degree of reversion than the offspring of a plant whose range in the reversionary scale is lower. At the same time certain facts observed in regard to the distribution of the various forms in the different beds suggest that, though the *heptandra* character is evidently transmitted to all the offspring, it is probable that the external conditions affect the precise degree in which this modification is exhibited. The facts were as follows:—

In the case of family 2 the mixed seed of several capsules had been divided into two lots, which were sown, pricked out, and planted separately, lot 1 in a narrow bed facing south, lot 2 in the middle of a bed facing east, and somewhat shaded to the south and west. The bed containing lot 1—a strip lying between a privet hedge and the path—was particularly dry and fully exposed to the sun. Out of a total of 27 classified plants in this bed only 4 eventually produced flowers with a normal or nearly normal corolla, while in as many as 16 of the remainder the late flowers were still of the *heptandra* form proper with 6 and 7 stamens. On the other hand among the 17 classified plants in the other bed, 8, *i.e.*, nearly half, eventually produced normal or almost normal flowers, and only 5 showed the *heptandra* form proper at the end of the season. Again in family 3, which had been similarly treated, the inequality in the distribution of the various grades in some of the beds was no less striking, though in this case the influence of the environment as a whole seems to result, in a lessening, rather than in an increase of the reversionary tendency in the more shaded lot of plants, as compared with those situated rather more in the open. Thus of 28 classified plants growing in a bed very much overshadowed by trees, only 1 eventually produced flowers at all approaching to normal, whereas in another lot planted a little more in the open all the 13 classified plants eventually produced flowers with a tubular corolla, and in 10 out of these 13 the late flowers were completely normal.

From the foregoing facts we may then conclude that the variety *heptandra* transmits its peculiar constitution to all its offspring, but the extent to which the abnormality is developed in an individual inheriting this disposition to heptandry may be in some degree influenced by external conditions, among which variations in amount of light and moisture are probably to be reckoned. Whether other factors are also concerned, and how far they may be opposed in their action, further experiment must decide. These conclusions are in harmony with the view held by Peyritsch[1] and others that the condition of peloria is also to some extent affected, if in some cases not actually induced by the stimulus of changes in the environment. So far as I am aware, however, no critical experiments on this point have as yet been carried out.[2]

It is further evident that the *heptandra* form is related to the type as recessive to dominant. Plants derived from the original *heptandra* parent but resembling the type—hence evidently crossbreds—invariably gave a mixed offspring, the numbers approximating to the ratio 3 Type: 1 *Heptandra*, or 1 Type: 1 *Heptandra*, according as they were fertilised with their own or sister pollen, or were crossed back with the *heptandra* form. Details of the breedings are as follows:—

(1). Nine of the putative crossbreds derived from the original *heptandra* plant were self-fertilised, and one of these individuals was also intercrossed with a sister plant. In all ten families the offspring were mixed; the total numbers obtained were 183 Type (including one plant showing slight abnormality in the first four flowers) and 49 *heptandra* (including ten plants with some normal or nearly normal flowers), where, on the basis of a 3: 1 ratio, we should expect 174 Type and 58 *heptandra*.

(2). Three of the crossbreds, of which two were among those self-fertilised in the preceding experiment, were crossed back with various *heptandra* individuals. The four resulting families were all mixed, the totals obtained being 69 type (including seven individuals with a few abnormal flowers) and 59 *heptandra* (iucluding six individuals with a few normal flowers) where we should have expected equality.

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[1] Untersuch. über die Aetiologie pelorischer Blüthenbildungen. Denkschr. d. k. Akad. Wien. Bd. XXXVIII.

[2] Gallardo's observation on the higher proportion of peloric individuals occurring among a batch of foxgloves grown under favourable conditions as regards space and illumination, as compared with another batch of similar origin, raised simultaneously, but less exposed to the sun and more crowded together, cannot be used as evidence in this connection, since the peloric parents were not apparently protected from crossing. Had intercrossing with type plants been prevented, all the plants in both batches would presumably have been peloric since peloria in the foxglove comes true from seed. (See Gallardo. Notes morphologiques et statisques sur quelques Anomalies héréditaires de la Digitale. Rev. gén. de Botanique XIII., 1901, p. 163).

Table showing the proportion of type and variety in each of the F_2 families derived from the putative crossbreds by self-fertilisation or by crossing *inter se*.

Reference number of family.	Form of Union.	Number of individuals in F_2 families.	
		Type.	*Heptandra.*
7	Crossbred × self	33	7
8	,,	21[1]	8[2]
9	,,	15	3[3]
10	,,	24	5
11	,,	13	8[4]
12	,,	22	5
13	,,	14	5[5]
14	,,	9	4
15	,,	11	1
16	Crossbred × sister crossbred	21	3
	Totals	183	49

A ratio of 3 : 1, calculated to the nearest whole number, would give 173 type and 58 *heptandra*.

[1] Including one individual with a few abnormal flowers.
[2] Including two individuals with a few normal flowers.
[3] Including one individual with a few normal flowers.
[4] Including three individuals with some normal or nearly normal flowers.
[5] Including four individuals with some normal or nearly normal flowers.

In the eight F_2 plants in which a slight abnormality in the first few (1-8) flowers was observed, the abnormality was in the form either of a lateral notch in the corolla edge, or of a longitudinal cleft which extended for a longer or shorter distance down one side. In other respects these flowers were normal as was also the whole of the rest of the spike. It is of interest to note that among the F_2 individuals classed as *heptandra* the proportion which eventually produced a few normal or nearly normal flowers was no higher, in one case rather fewer, when the *heptandra* form had been introduced twice into the pedigree than when the plants resulting from a first cross were self-fertilised or fertilised *inter se*. Thus the two crossbreds which produced plants of this grade when the breeding was in the form DR × R, yielded respectively four such plants in a total of twelve, and two in a total of nineteen, whereas on self-fertilisation the numbers obtained from these same crossbreds were respectively 1 in 3 and 2 in 8. (See families 8, 9, 17, and 18).

Table showing the proportion of type and variety in each of the F_2 families obtained from the crossbreds by crossing back with the *heptandra* form.

Reference number of family.	Form of Union.	Number of individuals in F_2 families.	
		Type.	*Heptandra.*
17	Crossbred × *heptandra*	10	12[4]
18	,,	26[1]	19[5]
19	,,	15[2]	8
20	,,	18[3]	20
	Totals	69	59

A ratio of 1 : 1 would give 64 type and 64 *heptandra.*

[1] Including five individuals with a few abnormal flowers.
[2] Including one individual with a few abnormal flowers.
[3] Including one individual with a few abnormal flowers.
[4] Including four individuals with a few normal flowers.
[5] Including two individuals with a few normal flowers.

In both experiments the results obtained point to segregation in accordance with Mendelian principles, the numbers recorded lying within the range of deviation which we might reasonably expect from the strict ratio 3 : 1 in the one case and 1 : 1 in the other.

Observations made in the course of the work on various characters unconnected with modifications of the corolla are briefly given below.

Fasciation and torsion of the stem were of frequent occurrence but of very varying degree.

Not a single case of peloria occurred among the whole number of plants raised.

It was noticed that certain families included a number of individuals of a bright green colour in marked contrast with the usual grey-green of typical plants. On investigation it was found that in these plants the stem during the greater part of its length was hardly hairy at all, and that the leaves were also much less hairy than usual. In two out of the six families in which these smooth plants occurred, the parents, both F_1 crossbreds, had been self-fertilised, and in both families the smooth plants were in excess of the hairy; the numbers recorded were six hairy and twenty-three smooth, and five hairy and thirteen smooth respectively, or almost exactly three smooth to one hairy. One or other of these two F_1 plants had also been used as a parent in the case of the other four families, but instead of being self-fertilised they were each crossed back with two different *heptandra* individuals. Each again gave a mixture of hairy and smooth, but the proportion of smooth was now greatly diminished, as shown below.

Comparison of the six mixed families derived from the two F_1 crossbreds (plants A and B) showed the following results:—

	Hairy.	Smooth.
Plant A × self gave	6	23
Plant B × self gave	5	13
Totals	11	36

	Hairy.	Smooth.
Plant A × *heptandra* plant 1 gave	29	16
× *heptandra* plant 2 gave	11	12
Plant B × *heptandra* plant 3 gave	13	9
× *heptandra* plant 4 gave	17	7
Totals	70	44

It is somewhat surprising, in view of the relation which experiments in other cases have shown commonly exists between the hairy and the smooth condition that the two sporting individuals in this case should have produced an *excess* of smooth plants on self-fertilisation. For an explanation of this result we must await the evidence from later generations.

The observations made in regard to the inheritance of flower colour are in entire accord, so far as they go, with the facts already published last year by Keeble, Pellew and Jones,[1] *viz:*

(1). That in all individuals whether white or coloured the lower lip is spotted, the spots being of various sizes.

It was noticed that in some families the spot area was occupied by large irregular blotches of colour, the appearance suggesting that a number of spots of ordinary size had become confluent. In one family this blotching was observed in ten out of the twenty-eight individuals recorded; in the remaining two families in which this peculiarity was seen the proportion was very much fewer. It is hoped to obtain evidence in regard to the inheritance of this character in the next generation.

(2). That among white flowered plants there are two kinds of individuals:—

(*a*) White-flowered plants with yellowish-green spots.

(*b*) White-flowered plants with red spots.

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[1] The Inheritance of peloria and flower colour in Foxgloves (*Digitalis purpurea*). New Phytologist, Vol. IX., 1910.

It was noticed that in many of the white plants with yellowish-green spots, the spots turned brown sooner or later, but the moment at which the colour change occurs, varied considerably. In some cases it occurred in the fully open but still unfaded flower, in others not until after the corolla had begun to fade, in others again while the corolla was still closed; in the latter case, however, the original yellowish-green could be seen in the younger buds.

(3). White-flowered plants with yellowish-green spots breed true, and even when faded show no sign of ground colour.

(4). White-flowered plants with red spots may either breed true or give a mixture of whites with red spots (dominants) and whites with greenish-yellow spots (recessives). The flowers frequently become tinged as they get older.

(5). In coloured plants the spots are always red.

Among plants of this class almost every shade could be found between deep purplish red and white with a faint flush.

SUMMARY.

1. The characteristic features of *D. purpurea heptandra*, viz., dialysis and staminody of the corolla appear to be transmitted by heptandrous plants to all their offspring.

2. The degree in which these peculiarities are exhibited varies not only among the individuals of a pure-bred family, but also among the flowers of one individual.

3. This variation in the case of the individual has the appearance of being due to a wave of reversion which advances steadily up to a point and then declines somewhat towards the close of the flowering period. Where the evenness of this wave-like advance is broken, as sometimes happens, it is probably due to an alteration in the condition of vigour at the level of the break. Such an alteration may well occur at the level of transition from a non-fasciated to a fasciated condition, or again, there may well be a difference in vigour between the upper region of a main axis and the simultaneously flowering base of a lateral branch.

4. The range of variation includes every grade from flowers with andrœcium and corolla normal, except for a lateral notch or cleft in the latter structure, to flowers *apparently* destitute of a corolla, and with nine or ten functional stamens united at the base, so that they form a single structure which falls as a whole.

5. Heptandrous individuals showing at first the extreme heptandrous condition (*i.e.*, no apparent corolla) may exhibit this

condition throughout or almost throughout the spike, or they may reach the *heptandra* condition proper which has a petaloid upper lip and seven stamens. Heptandrous individuals exhibiting this latter condition at the outset often produce eventually a few normal flowers.

6. The distinction between the variety *heptandra* and the type, in all individuals so far observed, is well defined. Where a heptandrous individual was found to produce a few normal flowers the heptandrous character was always evident throughout the rest of the long crowded spike, and conversely, a type plant with a notch or slit in a few of the lowest flowers would show a normal structure throughout the remaining length of the axis.

7. There is some indication that the degree of heptandry exhibited may be influenced by external conditions, among which variations in amount of light and moisture are probably to be reckoned.

8. The variety *heptandra* behaves to the type as recessive to dominant.

9. Two new forms appeared in the course of the experiments, *viz.*, one with stem and leaves nearly smooth, and one in which the spots on the lower lip of the corolla had fused to form large blotches. The inheritance of these two forms is being investigated.

The expenses incurred in the course of these experiments have been in part defrayed by a grant from the British Association for the Advancement of Science, and the use of the garden in which they were carried out was kindly permitted rent free by the Botanic Garden Syndicate.

I wish here to express my thanks to Miss D. F. M. Pertz to whom I am indebted for the drawings, and to Miss M. Pallis who kindly took the photograph.

EXPLANATION OF PLATE I.

ILLUSTRATING MISS E. R. SAUNDERS' PAPER ON INHERITANCE OF A MUTATION IN THE COMMON FOXGLOVE *(Digitalis purpurea)*.

Photograph showing *D. purpurea* type and variety *heptandra*, growing side by side in the same bed. Both are in full flower. The heptandrous plants show the numerous irregularly diverging stamens which give the spikes their characteristic appearance. In some of the flowers of the left-hand group the upper lip is becoming petaloid.

AN ECOLOGIST'S GARDEN.

By Macgregor Skene, B.Sc.

WITHIN the last thirty years or so a new conception has arisen of the uses to which a botanical garden may be put. The relations between the characters of plant, vegetation, and environment has been the object of a continually increasing volume of research, and this has impressed itself on botanical gardening. The development has followed two diverging paths. At the end of one is the magnificent new garden at Dahlem, near Berlin, which is due to the inspiration of Professor Engler. It is a collection of illustrations of the vegetation of different parts of the earth—is, in fact, a series of living "Vegetationsbilder": and provides at the same time materials for anatomical or morphological study on phytogeographical lines. The other leads to numerous alpine gardens scattered through the mountains of southern Europe, from the Austrian Tyrol to the Cevennes. These aim at giving opportunities for the exact ecological study of the organism. Among their number is the garden—or rather gardens—on Mount Aigoual, the second highest peak of the Cevennes.

Though only eight years old this garden on the Aigoual has reached a high state of development, and as well from its unique position as for the example it affords of what can be accomplished with limited material by means of devotion and energy, it seems to be deserving of introduction to the British botanical world.

The Aigoual is the dominant peak of the Southern Cevennes. Its geography may be most readily understood by imagining a horse-shoe of mountains with the limbs pointing eastward. The northern limb is the Grand Aigoual. At the eastern extremity it culminates in two peaks about three-quarters of a mile apart, and joined by a neck. The one to the east is the Pic de la Fajolle (5,083 feet), that to the west is the Aigoual (5,093 feet) on which is situated a meterological observatory. Westward the ridge slopes gently downwards for about two miles to the Col de la Sereyrède: the Col de la Sereyrède and the Col de Lesperou join the Aigoual to the southern limb of the horse-shoe—the Montagnes de Lesperou. The Col de la Sereyrède, it may be noted, is the watershed between the Atlantic and Mediterranean basins. Standing beside the forester's house, which is situated there, one sees to the north the Bonheur flowing towards the Tarn and the Garonne, and to the south the Hérault flowing to the Mediterranean. The Atlantic stream runs through an elevated valley, with gentle slopes and rounded outlines. The Hérault has cut itself a rugged gorge with almost precipitous sides. The difference is, of course, due to the much greater proximity of the Mediterranean, and no more striking illustration of this phenomenon of erosion could be found.

Geologically the Aigoual is composed of mica schists with frequent limestone bands. These are generally extremely firm, occur as lamellae in the schist, and are recognised by the type of weathering. But here and there bands of very considerable thickness occur—their position is frequently indicated by a disused limekiln—and these bands of precambrian limestone are one of the most interesting features of the mountain. Fifty years ago the Aigoual was entirely deforested: it was even possible to refer to its shining top as an example of the physical properties of mica-schist. Now, however, it is in active process of afforestation and is for the most part covered with plantations of larch, pine and fir.

The suitability of the situation for the establishment of an ecological garden is manifest when we note:—(i.) the geographical position between Atlantic and Mediterranean basins; (ii.) the elevation, which permits of a flora of the mid-European mesophytic type within fifteen miles of the markedly xerophytic Mediterranean flora; (iii.) the geological composition, which offers both calcareous and siliceous soils (it may be noted that granite occurs in the immediate vicinity); (iv.) the afforestation.

The idea of an experimental garden originated with M. Georges Fabres, the forestry inspector for the department, a man whose best monument is the reforested Aigoual. Thirty years ago he started making collections of various foreign trees round several of the stations. In 1903 the Director-General suggested to him and to Professor Flahault that a regular botanical garden might be laid out. Three sites were chosen. On the summit of the Aigoual it was found impossible to obtain satisfactory results owing mainly to the unceasing winds which swept it. A bog forming the source of one of the Atlantic streams has been utilised for experiments with such trees and shrubs as are willing to grow in very damp stations.

The third and most important—the garden proper—occupies about two acres of ground on the southern side of the mountains, It lies about 800 feet below the summit, at a point where the slope is less rapid than immediately above and below. It is, in fact, like the seat of an arm-chair, the back of which is formed by the mountain side below the neck, which joins the Aigoual to the Pic de la Fajolle. Two ridges close it in like arms. In front the seat narrows and ends in the precipitous valley of one of the tributaries of the Hérault. The garden bears the name "L' Hort de Dieu"—the garden of God. It was the highest point ever cultivated on the mountain, and from this fact is probaby derived the name.

In 1903 it was a mere desert, the typical mountain pasture of the Cevennes, a stretch of loose shingle with a miserable vegetation of *Festuca glauca* and *Sarothamnus purgans*: and for the transformation which has taken place since then Professor Flahault is responsible. A laboratory had to be built and its foundations were laid on the site of an old "bergerie" which had sheltered shepherds and their flocks in the early years of last century. Modern science and ancient romance come into contact; for in this very "bergerie" did Jean Cavalier nurse his wounded and store his arms, and from it his lieutenant Castanet descended on Valleraugues to secure hostages for his captured wife.

"And O, how deep the corn
"Along the battlefield."

The situation of L' Hort de Dieu made the start very difficult. Before the laboratory was built Professor and labourers alike had a walk of nearly five miles to and from their daily task. Even now the nearest baker's shop is five miles away, and the postal service sometimes ceases to be a matter for jesting. Despite all difficulties, however, progress has been rapid. The laboratory is a building of the solidity necessary to withstand the storms of autumn: it is capable of accomodating about a dozen people. Beside it there is a bothy for the labourers. During the erection of these buildings the garden itself was not neglected. To clear the ground of *Sarothamnus purgans* was the first task, and it was no light one. Then it had to be prepared for planting the trees: the process is simple enough under ordinary conditions, but L' Hort de Dieu was entirely denuded of humus, and on the Aigoual there was no manure of any kind. Weeds from the road used to be carefully guarded and deposited in a hole to serve in the future as leaf-mould. The planting went on, however, and at the end of three years over 6,000 seedling trees had been put into the ground: rockeries had been built : an experimental kitchen garden had been laid out : and a whole series of pasture plots, under various conditions, were under observation. Nor must we forget the director's particular hobby: a mile-and-a-half of well-planned and well-kept paths traverse the garden in all directions. Irrigation is carried out by means of about half-a-mile of canals fed by numerous springs.

Such is the situation of the garden and its history. What of its present state? It is naturally divided by the little streams which run through it: and the divisions represent the three continents—Europe, Asia, America. Each division contains the plants, and more particularly the trees, proper to it. The trees are planted according to the best methods of French forestry in specially prepared little terraces on the hill-side after the *Sarothamnus purgans* has been cleared away. In this department of course results are slow to come, but already it is possible to say of many trees whether or not they can be planted with hope of success. The main object is to find out those suitable for forestry purposes on the high mountains of southern France, with special reference to foreign species.

To take concrete examples: comparisons are being carried out between *Abies cephalonica* (Grecian Mountains), *Abies Pinsapo* (Spain-Sierra Nevada), *Abies Nordmanniana* (Asia Minor) and *Abies pectinata*: between *Cedrus Libani* (Palestine) and *Cedrus Deodara* (Himalayas): *Alnus incana*, *Alnus viridis* (North temperate regions), *Alnus surrulata* (North America), and *Alnus glutinosa*. Here it may be noted that results obtained at L' Hort de Dieu are correlated with facts ascertained from the collections round the forestry stations already mentioned. The plantations of young trees are supplemented by numerous rockeries of herbaceous plants and shrubs.

To this more special aim must be added the study of the general ecology. Again to take concrete instances: *Castanea sativa* finds its natural limit at 3,410 feet on the southern slopes; at this level it is replaced by *Fagus sylvatica*, and the why and wherefore of this transition—a very sharp one—is a question of great interest. *Quercus sessiliflora* is spontaneous to about 4,200 feet but does not produce fruit at this elevation—the problem offered still awaits solution.

Naturally ecological observation is not bounded by the limits of the garden, in fact the whole mountain is like one gigantic experimental plot. On it may be studied the reason of the failure of *Pinus sylvestris* and of the success of *Pinus montana*. The effects of snow and wind are exhibited with diagrammatic clearness. The effects of grazing animals are no less evident than annoying. A well-marked limestone flora is developed on the limestone bands. The connection between afforestation and water supply is a larger problem, and one of immense importance to the "Midi," and a comparison between the exploits of the Hérault in the way of destruction during the palmy days when the Aigoual was a shining mass of mica schist, and its present insignificant attempts, is instructive.

But the aims of L' Hort de Dieu are wider yet. There is an experimental kitchen garden, and a series of plots designed for the culture of ornamental plants. And finally there is a series of pastures ranging from the original stony wilderness, through plots from which the stones have been removed, irrigated plots, plots manured by grazing animals, to plots scientifically treated with artificial manures. The vegetable garden, the ornamental plots and the experimental pastures are primarily designed to show a very ignorant highland population what can be done with the means at its disposal.

One who has enjoyed, as has the present writer, a month's hospitality in this veritable garden of the gods, must find it difficult to refrain from launching into a panegyric of all which its name calls up in his mind. But no praise could seem otherwise than cold to the writer and fulsome to the reader. It may be added however that the opportunities for work are as varied and abundant as the life is simple and refreshing.

The above description is all too inadequate, but may serve to bring to the notice of our British botanists, a garden which is not only a model of what such a garden ought to be, but also a striking example of the results attainable without great means, but with the qualities exemplified by Darwin's motto—It's dogged does it: and of a most admirable catholicity of aim and ideals.

NOTE ON AN ARTIFACT IN THE WALLS OF THE CELLS OF THE MEDULLA IN THE LAMINARIACEÆ.

By M. G. Thoday (formerly Sykes).

[Text-Figs. 13 and 14].

Girton College, Fellow of Newnham College, Cambridge.

It was recently pointed out to me by Miss E. R. Saunders, that in a section of *Laminaria digitata* in the collection at the Balfour Laboratory, Cambridge, the elements of the medulla showed a most characteristic *reticulate thickening* on their longitudinal walls.

This reticulate thickening (see Figs. 13 and 14) was well developed in the walls of both the primary pith filaments[1] and the hyphæ, but was not present in the much thinner walls of the secondary sieve tubes.[1] The "thickenings" extended even into

[1] For use of terms see Sykes, M. G., "Anatomy and Histology of *Macrocystis pyrifera* and *Laminaria saccharina*"; Ann. of Bot., XXII., 1908, pp. 309, 310 and 300-303.

the dilated parts of the elements almost up to the transverse wall or sieve plate.

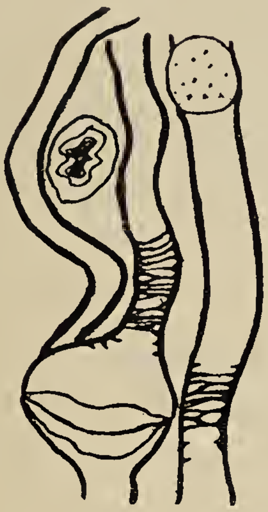

Fig. 13.

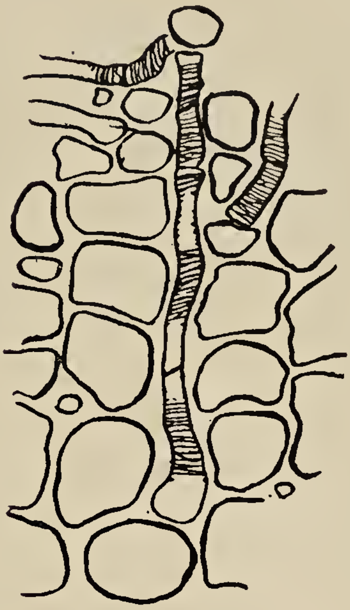

Fig. 14.

Fig. 13. *L. digitata*; three of the longitudinally running element of the medulla. (Preserved in strong alcohol).

Fig. 14. *L. digitata*; part of a transverse section showing some of the invading cortical hyphæ. (Preserved in Carnoy's fluid).

Similar appearances have been noted from time to time in material examined at the Cambridge Botany School, and it seemed advisable to try to arrive at an understanding of their nature. The material from which Miss Saunders' slide had been prepared was preserved in strong alcohol. Material of an old stipe of *L. digitata* preserved in Carnoy's fluid was also examined, and showed the "thickenings" equally strikingly developed. Faint indications of similar "thickenings" were found in the stipe of a young sporeling of *L. saccharina* preserved in 70% alcohol,[1] where the walls of the medulla cells are as yet comparatively slightly mucilaginous and swollen.[2] The "thickenings" always stain in the same way as the rest of the inner layers of the cell-wall; deep blue with methylene blue, faintly with Congo red, etc.[3]

It was found that the demonstration of these "thickenings" depended entirely on the methods followed in preserving, staining, mounting, etc. An old stipe of *L. digitata* in sea-water was kindly sent to me by Professor Yapp, and was examined while still fresh; no such appearances were then present in the cell-walls. They could, however, be produced by drying, or by partially dehydrating the sections in alcohol. Material of *L. digitata*, *L. saccharina* and *Macrocystis* preserved by killing and fixing entirely in aqueous solutions, without the use of alcohol, showed little or no trace of these "thickenings"; in sections obtained from the material preserved in Carnoy's fluid the "thickenings" were made to disappear by placing in swelling agents, such as iodine dissolved in an aqueous solution of potassium iodide, or dilute glycerine, owing to the absorption of water by the mucilaginous walls.

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[1] Ibid, p. 309, Stage 1.

[2] Oltmanns. "Morphologie und Biologie der Algen," Jena, 1904, I., p. 446.

[3] Sykes, M. G., l.c., p. 312.

The very definite appearance of reticulate thickenings in material preserved in alcohol is thus apparently entirely due to *wrinkling* consequent on partial dehydration, and since it begins to appear after very slight drying it affords a remarkable indication of the very mucilaginous nature of the longitudinal walls of the medulla cells in their normal state. At the base of the stipe, where all the cell-walls of both cortex and medulla become much thickened and cartilaginous, this wrinkling does not occur on drying.

NOTES ON RECENT LITERATURE.

Graf Solms Laubach on the Petioles Attributed to *Cladoxylon* and *Medullosa* (*Steloxylon*) *Ludwigi*."

In April, 1909, attention was drawn in these pages to M. Paul Bertrand's conclusion that the Botryopteridean petiole *Clepsydropsis* was borne on stems known as *Cladoxylon* and *Steloxylon* (*Medullosa*) *Ludwigi*. In the following year Graf Solms Laubach denied that *Clepsydropsis* was the petiole of either of these stems.[1] This writer points out that he had previously described a petiole still attached to a *Cladoxylon* stem, and that this petiole differs markedly from *Clepsydropsis*. The vascular bundle of this *Cladoxylon* petiole forms a band, narrowed in the middle and transverse to the axis; this band has on one side two projections and appears to contain four protoxylem groups, two more or less in the basal part of the projections and two immersed in the wood near to the ends of the band. In the petiole known as *Clepsydropsis*, however, the two projections are wanting and there are but two protoxylems in the loop-like gap in the swollen ends of the vascular band that forms the petiolar strand. It is fair to add that Graf Solms Laubach admits that the position of the protoxylem is not quite clear in the petiole described by him. Moreover it is unfortunate for comparison with the Botryopterideæ that neither in his present communication nor in the earlier paper to which he refers is it quite clear whether the two projections of his two *Cladoxylon* petiole face adaxially or abaxially.

As regards the attribution by M. P. Bertrand of *Clepsydropsis kirgisica* to *Medullosa* (*Steloxylon*) *Ludwigi*, the petioles of this species figured by Graf Solms Laubach are remarkable for the extraordinary, almost unparalleled, variety of their vascular bundles in cross section. They certainly do not resemble *Clepsydropsis*. The species is regarded as belonging to the Medullosæ, but not to the genus *Medullosa*.

I.B.

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[1] Zeitschrift für Botanik, Heft 8, Jahrgang, 2, 1910.

The Journal of Genetics.[1]

The Journal of Genetics, which is edited by Mr. Bateson and Professor Punnett, is to be devoted to the "publication of records of original research in Heredity, Variation and allied subjects." Those whose special interest lies in the subjects with which the Journal is concerned will appreciate the convenience offered by a recognized medium for the publication of such records, which have hitherto appeared in a variety of publications, some of them not very readily accessible to many students.

The prospectus of the new Journal announces that "adequate illustration will be provided, and, where the subject matter demands it, free use will be made of coloured plates." In view of the prominent position which has been taken by investigations into the inheritance of colour, the coloured plates should prove a most useful feature of the Journal. It is often essential that the reader should be able to recognize with some precision the different tints with which the author is dealing; yet the terminology applied to colours is much lacking in precision, and confusion is particularly liable to occur in the rendering of English terms into other languages, and *vice versa.* The difficulty has only been partially overcome by the use of standard Colour Charts, partly because of the difficulties introduced by differences of texture, partly because it is only rarely that the colour is the same over the whole area of the pigmented part.

The first number of the Journal, which was published in November last, contains five papers. In the following notes no attempt is made to deal completely with the subject matter of these contributions, but attention is called to some points of general interest.

Professor Keeble and Miss Pellew have two papers, one dealing with the "White-flowered varieties of *Primula sinensis*," the other with the "Mode of Inheritance of Stature and of Time of Flowering in Peas." The first paper records the discovery of a new type of white-flowered *Primula*, in which the colour-factors are lacking from the flower, although present in the stem. This red-stemmed *recessive* white must be distinguished from the more familiar red-stemmed *dominant* whites, in which the white flowers are due to the action of factors which prevent the actual development of pigment in the flower, even though the factors necessary for the production of coloured flowers are present.

In the second paper by the same authors evidence is brought forward which indicates that stature in certain Peas depends upon two factors, one determining the thick stems, the other the long internodes; and, further, that there is a definite relation between these vegetative characters and the time of flowering, the great majority of thick-stemmed plants being late in flowering.

Dr. Salaman contributes an extensive memoir on inheritance in domestic and other varieties of the Potato. Certain points of great interest arise out of his experiments with *Solanum etuberosum.*

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[1] "The Journal of Genetics," edited by W. Bateson, M.A., F.R.S. and R. C. Punnett, M.A. Cambridge University Press. Price 30/- per volume; separate parts 10/- each, net. Vol. I., No. 1, November 18th, 1910.

Solanum etuberosum had been grown at Reading for more than twenty years, and had remained completely sterile. In 1906, however, Mr. Sutton obtained seed from one plant, and Dr. Salaman, working with plants of the same race, succeeded in making a cross. In the following year fertile seed was again obtained by both investigators. During the period of sterility, the parent plant had become noted for its immunity to the attacks of *Phytophthora infestans*, but a large proportion of the seedlings to which it gave rise were attacked by the fungus. The proportions in which the susceptible and immune seedlings occurred suggest that immunity is a recessive character; if this should prove to be the case, it is interesting to notice that the heterozygous parent remained immune as long as it was sterile.

Solanum etuberosum presents another point of interest in that it is found to differ from the domestic varieties in regard to the dominance of certain characters. Thus, in *S. etuberosum*, the round shape of the tuber is dominant to the long shape, the shallow eye is dominant to the deep eye, and the white is dominant to the dark purple colour. In the domestic varieties exactly the reverse is true in each case.

Miss Saunders' paper on the "Inheritance of Doubleness in Flowers," deals with the production of double flowers in *Petunia.* It is found that singleness is a dominant character; cross-bred singles, however, when self-fertilized, produce only singles; while singles crossed with the pollen from doubles yield doubles in the first generation. It is clear that in *Petunia* gametogenesis is of the peculiar type which Miss Saunders has already shown to occur in the Stocks (*Matthiola*), where the factors for singleness and doubleness are distributed differently among the ovules and the pollen grains. Thus, the pollen of the singles is homogeneous as regards the presence of some factor necessary for the production of single flowers; while, with regard to the ovules of the singles and the pollen of the doubles, the results obtained are such as would occur if either (1) the ovules were homogeneous and the pollen heterogeneous as regards the absence of some factor for singleness, or (2) the ovules were heterogeneous and the pollen homogeneous in respect of this factor.

The paper by Mr. Doncaster and Mr. Marshall is concerned with a problem relating to the determination of sex. The opinion has been somewhat widely held that in mammals one ovary produces eggs which will give rise to females; the other, eggs which will give rise to males. The authors have tested this hypothesis in the case of the rat by performing one-sided ovariotomy upon two female rats. Each of these animals subsequently produced a litter of young, and each litter contained young of both sexes. It is clear, therefore, that the "right and left" hypothesis does not hold for the rat, and its definite disproof in this case detracts from the probability of its holding good in the case of other mammals.

R.P.G.

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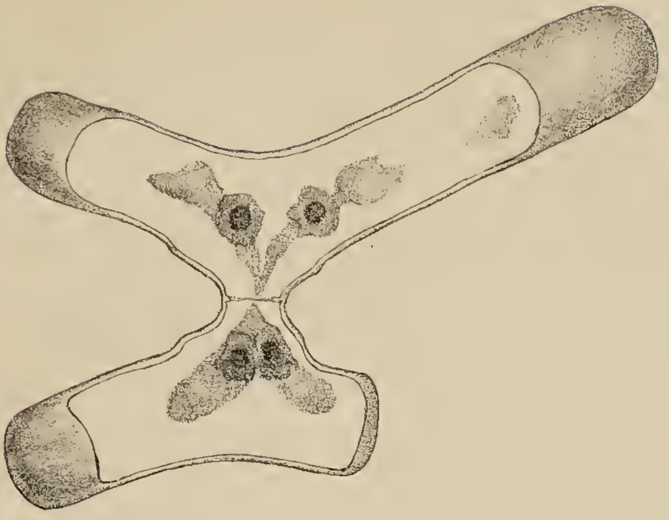

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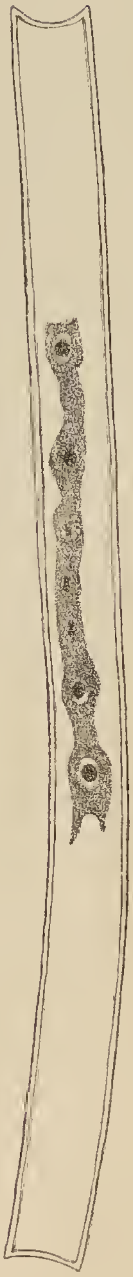

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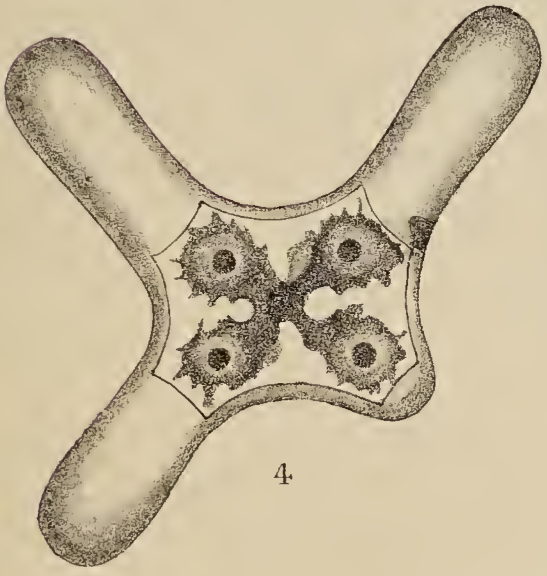

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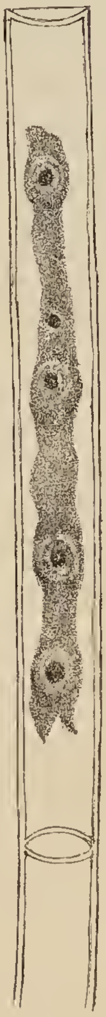

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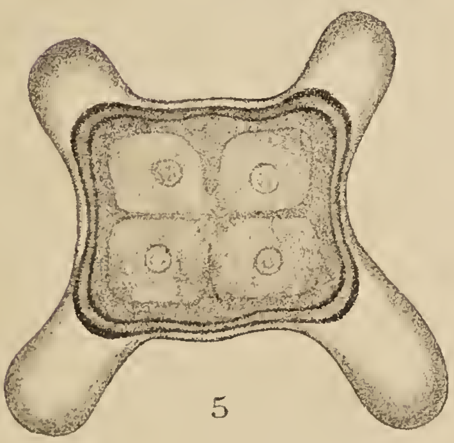

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THE
NEW PHYTOLOGIST.

VOL. X, NO. 3. MARCH, 1911.
[PUBLISHED MARCH 31ST].

FLORAL EVOLUTION; WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

BY H. F. WERNHAM.

I. INTRODUCTORY.

IN the following brief review of that group of Angiosperms in which a definite corolla, composed of united petals, is present, an attempt is made to discover and to display some of the broader evolutionary principles or tendencies which underlie floral development, as reflected by the various members of that group.

It will be necessary, at the outset, to discuss in broad general outline the purpose and nature of these tendencies; in other words, the initial problem before us is the biological history of the flower.

The typical flower is an aggregate of sporophylls delimited by a perianth; the perianth, in most cases, determines the individuality of the flower. We call a buttercup a single flower because it comprises a number of sporophylls associated with a single perianth; a daisy, on the other hand, although it consists of a number of sporophylls associated with a very definite perianth-like aggregate of floral and involucrate leaves, is regarded as an inflorescence, a "head" of many flowers, because the sporophyll aggregate is capable of sub-division into a number of definite sets or units, each associated with a perianth.

In the attempt to unravel, from the host of floral forms with which we have to deal, one or more continuous evolutionary threads upon which these forms may be strung in progressively ordered arrangement, we need at the outset to fix upon some starting point; in other words, we must try to obtain an idea, more or less definite, as to what characters are to be regarded as primitive in descent, and what as specialized.

What, then, is the general aspect of the primitive flower?

The evolutionary origin of the angiospermous flower has formed the subject of a vast amount of discussion; and this latter has been rendered largely abortive by reason of the extreme paucity of the geological record. We have been driven, in consequence, to the comparative study of existing forms in the search for light upon this all-important question. This study has been combined as far as possible with fossil evidence, but the result has, for reasons which will be suggested presently, proved far from satisfactory.

The views respecting the primitive flower seem to have fallen into two main groups, determined, in the first instance, by emphasizing the individual sporangium, and in the second instance, by emphasizing the sporophylls. If, for the sake of clearness, we may anticipate for a moment, the former set of views contemplates, as a primitive flower, a single sporangium borne terminally, and naked,—*i.e.*, unassociated with a perianth; while the latter has for its primitive flower an aggregation of sporophylls, some fertile and some sterile, all indefinite in number, and arranged upon an axis more or less elongated, in a manner analogous to the arrangement of the vegetative leaves.

The contemplation of the individual sporangium has, it is urged, been unfortunate in its results, so far as the evolutionary history of the flower is concerned. This point of view would appear to have arisen from the burning question of the evolution of the seed. In this latter question, emphasis has necessarily been laid upon the individual megasporangium; and geology, so sparing in its assistance to the solution of the past history of the flower, has proved abundantly generous in its guidance where the problem of the seed habit has been concerned.

The gulf does not at first sight appear to be a wide one between the female sporocarp of *Azolla* and the female flower of *Najas*. In both we have a single megaspore enclosed within its sporangium; the sporocarp wall in the former is readily regarded as the analogue, if not the homologue,[1] of the integument in the latter, while a perianth is absent in both cases. We have only to suppose fusion between the sporocarp and sporangium walls in *Azolla*, together with infolding of the sporophyll to form a closed chamber, to produce the *Najas* flower, or something nearly resembling it. Closer consideration, however, appears to cast serious doubt upon the propriety of regarding the apparent narrowness of this gulf as

[1] Çelakovský.

having any real significance. In the first place, the vegetative system of *Najas* suggests that it, like so many other flowering aquatic plants, is probably the reduced descendant of terrestrial forms. Again, although the female flower is naked, the male has a perianth; this surrounds a single anther, and the male flower is therefore, like the female, represented by a single sporangium. The case is very different with the male sporocarp in *Azolla*, where an indefinite number of microsporangia are borne upon a central columella. Which of these two are we to regard as the more primitive character, the solitariness of the female sporangium, or the aggregation of the male sporangia in indefinite numbers? We shall return to this point later.

Mention should be made, too, of the presence of three styles in the female flower of *Najas*, suggesting the derivation of the ovary from three carpellary leaves. If this be the case, we are face to face with characters the reverse of primitive, namely, the fusion of sporophylls, and the association of but one sporangium with three sporophylls. We search in vain outside the Angiosperms for indications of such characters; although at the same time, the details of development in the ovary of *Najas*[1] leave the question somewhat open as to whether the structure enclosing the ovule is the true homologue of sporophyll tissue, as it is unquestionably in the case of many wide groups of Angiosperms to be referred to shortly. Lastly, the anatropy of the ovule in *Najas* has no little weight in throwing doubt upon the primitiveness of this form.

One or two members of the Piperaceæ have been selected, with more reasonable justification perhaps, as representing primitive types illustrative of this first group of views. In *Peperomia*, for instance, the spadiciform inflorescence is composed of definite hermaphrodite entities, properly termed "flowers" although they are naked, each being subtended by a bract. The ovary encloses a single basilar orthotropous ovule, and each pistil is associated with two or more stamens.

The female portion of this flower is thus free from the more obvious objections to primitiveness, which we have noted in *Najas*; and although the Piperaceæ display a considerable amount of plasticity morphologically, the habit of these plants is not so specialized as that of the flowering aquatic. Other details of structure, moreover, such as the presence of perisperm and the number of nuclei in the developing embryo-sac,[1] have been advanced in support of the primitiveness of these piperaceous forms.

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[1] Rendle. "A Systematic Revision of the Genus *Najas*." Trans. Linn. Soc. Ser. ii. v. 379, 1899.

Apart from a general objection to the primitiveness of a solitary sporangium, to be referred to later, it is pointed out in the case of the Piperaceæ, that the species which comprise this natural order display considerable variety in the number of their floral parts. In the andrœcium, we meet with the numbers 2, 3, and 6—∞; in the gynæcium, the ovary is crowned in some cases by two or more styles, indicating the presence of more than one carpel,—a condition comparable with that which obtains in *Najas*. In the allied natural order, the Saururaceæ, moreover, a more or less indefinite number of stamens is associated with 3 to 5 subapocarpous carpels, and in cases where the ovary is unilocular, several ovules may be present. And lastly, in Saururaceæ, and in an allied group, the Chloranthaceæ,[2] the ovary is sometimes inferior.

This variability within a close circle of affinity leaves the question an open one, on general grounds, as to whether the solitary or the aggregated state of the sporangia be relatively primitive.

But broader considerations seem to outweigh the evidence afforded by minor detail. We meet with no cases of solitary sporangia in the reproductive organs of Vascular Cryptogams,[3] and the solitary condition is decidedly the exception in the Gymnosperms. The higher reproductive units—strobili, sori, cones—and their general occurrence throughout these last-named groups, all point to aggregation of sporophylls and sporangia as a condition firmly established before the advent of the Vascular Cryptogams in the course of the evolution of plant forms.

Again, the solitary ovule is frequently, if not prevailingly, shared between two or more sporophylls,[4] and the component carpels are fused together to form the unilocular ovary. We can suggest no parallel to either of these conditions outside the Angiosperms; and this fact would appear to weigh not inconsiderably against the suggested primitiveness of those groups which Engler has placed at the base of the Archichlamydeæ, and which are represented chiefly by the so-called Amentiferæ, and the Urticales. In these groups, the female organ consists typically of a single ovule associated with two syncarpous carpels.

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[1] See Johnson. "On the Development of certain Piperaceæ." Bot. Gaz., xxxiv, 321, 1902; also

Brown. "The Nature of the Embryo Sac of *Peperomia*." Bot. Gaz. xlvi, 445, 1908, where the relative literature is cited.

[2] See Armour, in THE NEW PHYTOLOGIST, vol. V., p. 49: "On the Morphology of Chloranthus.

[3] The female sporocarp of *Azolla* seems to afford the single exception to this statement.

[4] *Supra*. p. 75.

These considerations seem to afford no little justification for regarding the solitary state of the sporangium as a character not primitive, but the result of reduction. This reduction is intelligible enough, biologically, for it reflects one of the chief guiding principles of vegetable evolution, which we will now proceed to discuss in turn. This principle we may name

1. The Tendency to Economy in Production of Reproductive Parts.

This principle is strikingly illustrated by the enormous reduction observable in the gametophyte, and in the megaspore output, as we pass from homosporous to heterosporous forms. Economy is the keynote of the progress to heterospory, and of its outcome, the seed; we shall endeavour to illustrate, from the series of Angiosperms, that economy is also a guiding principle in the evolution of the flower.

Our floral prototype, then, will be one in which the principle of economy is realized the least, and will therefore consist of an indefinite number of sporophylls, borne upon an axis more or less elongated, and repeating in their arrangement the succession of the vegetative leaves. Analogies are not far to seek; they are common enough in the Gymnosperms; in the Firs, we find cones composed of an indefinite number of sporophylls arranged spirally like the vegetative leaves; in the Cupressineæ, sporophylls and vegetative leaves are borne typically in decussating whorls.

Perhaps the most striking analogy to this floral prototype is afforded by that interesting fossil group the Bennettiteæ. The "flower" of *Cycadeoidea ingens*, figured by Wieland, and reproduced in Scott's "Studies," p. 584,[1] consists, proceeding from below upwards, of an indefinite number of sterile bracts, followed by an equally indefinite number of complex frond-like male sporophylls; these are surmounted by the megasporangia, borne in large numbers upon the elongated continuation of the main axis.

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[1] Second edition, 1910.

The step from this "flower" to the flower of many members of the cohort Ranales[1] appears at first sight to be but small. But the very definite angiospermy of the latter and the equally definite gymnospermy of the former are separated by a gulf which research has failed hitherto to bridge, and at which speculation must halt for the present. The peltate, closely approximated inter-ovular scales in the bennettitean "flower" may, it is true, represent carpels which are on the way to the angiospermous condition; but in any case these "carpels" are highly specialized, and very different from the typical female sporophylls of Angiosperms.

We can venture to say no more in this connection than that angiospermy, like other biological characters, may have been acquired in more ways than one in descent; and that the Angiosperms represent the type so far successful that only the merest traces of other types—*e.g.*, Bennettiteæ—remain to us in the fossil record.

Our purpose, however, is to follow the history of the flower subsequently to the establishment of angiospermy, and not to enquire into the origin of the latter phenomenon. *Cycadeoidea* affords a useful analogy, if nothing more, from the point of view of the principle of economy in the number of reproductive parts; for it is, relatively to the Angiosperms, a primitive form with an undoubted filicinean ancestry, and has, at the same time, indefinite numbers in its reproductive organs.[2]

In the Magnoliaceæ[2] the arrangement of the flower is essentially the same, typically, as in the case of the *Cycadeoidea* described above; the perianth comprises an indefinite number of leaves, and the stamens and carpels are borne, spirally arranged, upon an elongated axis.

The progression along the line of reduction in the number of parts may be well illustrated by the typical floral formulæ for the largest[3] natural orders of Ranales exhibited in the following table:—

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[1] The names of the cohorts and natural orders used throughout this paper are those of Engler's classification, unless otherwise specified; and Willis's *Flowering Plants and Ferns* will be found convenient for purposes of reference to the details of this system.

[2] See Newell Arber and Parkin. Journ. Linn. Soc. xxxviii. 29, 1907.

[3] Excluding Lauraceæ, which Engler groups with Ranales, and in which the component parts of the flower are definite in number.

	Symmetry.	Perianth.	Andrœcium.	Gynæcium.
Magnoliaceæ	Spiral	∞	∞	∞
Anonaceæ Ranunculaceæ	Hemicyclic	3+3+3 Definite	∞	∞
Menispermaceæ	Cyclic	3+3+3+3	3+3	3
Berberidaceæ	Cyclic	3+3+3+3	3+3	1

Moreover, the working of the same principle of economy is observable, in many cases, in the series of genera comprising each natural order of Ranales.

Let us now examine briefly the broad biological significance of this principle of progressive economy in production of parts. General decrease means decrease in the number of male and female organs, and therefore, *ceteris paribus*, a decreased chance of pollination. But natural selection would clearly not permit of any interference with the efficient performance of one of the principal vital functions; the result is that a second principle has been called into operation in order to make possible the economy of the first one, ensuring that an increased chance of pollination, rather than the reverse, shall accompany the general tendency to oligomery. This second principle we may name the tendency to

2. Progressive Adaptation to Insect Visitors.

From a general study of the various floral types, it is gathered that these two are the fundamental tendencies in the evolutionary history of the flower, and we hope to illustrate their working in the sequel.

First, however, attention must be called to one or two important tendencies which subserve the two fundamental principles named.

(a). In the first place we have the well-recognized tendency to increased *conspicuousness* either (a) by enlargement of the individual flower, or (b)—and this is the more wide-spread—by the aggregation of flowers into progressively dense inflorescences by active branching of the floral axes. The first experiment, so to speak, in the direction of increasing conspicuousness is reflected in the petaloid perianth, which represents one of the principal steps from *Cycadeoidea* to the Magnoliaceæ. Heterochlamydy, the differentiation of the perianth into a protective calyx and an attractive corolla, doubtless went hand in hand with the same tendency.

For the sake of completeness in the tentative formulation of these evolutionary principles, it will be necessary at this stage, somewhat out of place perhaps, to call attention to a phenomenon characteristic of many of the more advanced groups of Archichlamydeæ, namely, indefinite numbers in the andrœcium. The groups concerned are, approximately speaking, comprised in the cohorts Centrospermæ, Rhæadales, Parietales, Opuntiales, and Myrtifloræ. This indefiniteness is regarded by many, if not by all, as primitive, and Celakovsky in his masterly paper, *Das Reductionsgesetz der Blüthen*, etc.,[1] has described a considerable number of types in support of this view. In other respects, particularly in the gynæcium, many of these flowers are undoubtedly of a relatively advanced type; and if the number of stamens be regarded as primitively great, and compared with the andrœcium of the Ranales, we must suppose that the andrœcium has in many cases lagged behind the gynæcium in the course of descent.

This, of course, is by no means an improbable view, but no general biological considerations have, to the writer's knowledge, been urged in its support; and a phenomenon so extensive seems to call for some explanation. An alternative aspect of the question is presented below; but it must be premised at the outset that the aspect is based only upon speculation, and much minute research into the structure and development of a host of forms is necessary before any hope of a definite decision can be entertained. In any case, however, the matter is not one of primary importance for our present purpose, which is to furnish an introduction to the study of the Sympetalæ; for among these flowers an indefinite andrœcium is an extremely rare feature.

We have selected the typical Ranalian flower, with indefiniteness in the numbers of all its parts, as a starting-point from which to trace the working of our principles; we would urge, however, that all flowers—such for instance as the Cactus—which have a large number of perianth segments, stamens, and carpels, are not therefore necessarily primitive. In a large number of cases this indefiniteness has resulted from chorisis in descent of the parts of oligomerous ancestors, in a manner analogous to the partition of the vegetative leaves.

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[1] *Sitz. der Königl. Böhmischen Ges. der Wiss.* Prag. 1895, pp. 1—140.

It is here suggested that this tendency may be due to the extension of the active branching of the floral axes to form dense aggregates of flowers to the parts of the individual flower itself. It may, of course, be objected against such a supposition that in the groups where the highest expression of floral aggregation is reached (the Compositæ, for example) there is no indication of chorisis. In reply to such an objection, we may premise that it is in the less specialised Archichlamydeæ that the principle of economy, and the tendencies which immediately subserve it, is seen in the fullest activity of its working; while in the Sympetalæ, as we hope to show, oligomery is virtually a fixed character, progression taking principally the line of adaptation to insect visitors. In other words, the polypetalous forms constitute, as it were, an experimental ground for evolution; in the Sympetalæ, on the other hand, the tendencies are more fixed and definite; and in the Compositæ, which comprise considerably more than one quarter of the total number of species of Sympetalæ, the climax of oligomery combined with insect-adaptation has been attained, the enormous number of species of this very natural group affording indisputable evidence of its success in the struggle for existence.

Returning now to the enumeration of the subsidiary tendencies, we may dismiss the first, conspicuousness, with the comment that it subserves, of course, the second fundamental principle, that of adaptation to insect-visitors.

(b). Devices of floral structure and habit, in obvious relation to insect-visits, represent a second tendency subsidiary to our second fundamental principle; and pre-eminent among these, as being of the most general occurrence, is the tendency to *zygomorphy*. This, we shall find, is a condition relatively rare in the Archichlamydeæ as compared with the Sympetalæ—as we should reasonably expect, according to the lines we have laid down. Zygomorphy may be the direct result, so to speak, of insect-visits, as is the case with zygomorphic flowers which are relatively large and solitary, or, at any rate, members of more or less lax inflorescences. More generally, however, zygomorphy appears to follow upon aggregation into dense inflorescences, the outer florets becoming more or less strongly zygomorphic, largely as the direct result of the mechanical conditions of development. Examples of this will present themselves readily to the reader's mind; but the two most significant are afforded by the Umbelliferæ, which, for many reasons, may be placed at the head of the main evolutionary line of Archichlamydeæ, and by the Compositæ, the highest type of flowering plants.

(c). A third, and perhaps the most important, subsidiary tendency is that of *Fusion of Parts.* This subserves both the fundamental principles. In the first place, space is economized by fusion ; economy, too, is effected in material, as is the case with the fusion of carpels with receptacle in the Calycifloræ of Bentham and Hooker. Material is saved, too, in the shortly filamented or subsessile anthers of epipetalous forms. The same primordia, again, may suffice for the members of a fusion, as is exemplified in the development of the petals from the dorsal portions of the stamens observed in certain Primulaceæ.

In the second place, fusion to form a *tube* is connected with the concealment of honey, and so with the principle of adaptation to insect-visitors. The primary division of Dicotyledons into polypetalous and sympetalous forms therefore becomes significant in the light of these principles, and they go far in the direction of justifying this division as a truly natural one.

Other, less general, fusions connected with adaptations to insects are seen in the staminal tubes of some forms, *e.g.*, the Papilionatæ and the Geraniales, and in the adhesions met with in various highly specialized groups, such as the Asclepiadaceæ.

In view of the primary importance, in what is to follow, of the general considerations to which we have drawn attention in the present paper, it will be well, perhaps, to conclude the latter with a brief summary :—

1. The fundamental guiding principles in the progressive evolutionary history of the dicotyledonous flower are two in number, *viz.* :—

    (i). Economy in production of the several items comprising reproductive organs.

    (ii). Progressive adaptation to the reception of insect-visitors.

2. The second of these principles compensates the first for the decreased chance of pollination which the latter involves.

3. There are also certain tendencies which subserve these two main principles, the most wide-spread being :—

(i.) Progressively increasing *conspicuousness* attained either:—

(a.) By enlargement of the individual flower, or, as is by far the more general case,

(b.) By excessive branching of the floral axes to produce *aggregation* of the flowers into dense inflorescences. This branching tendency has not impossibly extended itself, in many groups of the Archichlamydeæ, to the parts of the individual flower, thus constituting a *Secondary Branching tendency*, resulting in secondary indefiniteness in the numbers of the floral parts.

(ii.) Devices of floral structure or habit which have obvious relation to insect-visits; chief of these, and the only one of such general occurrence as to be named a tendency, is *Zygomorphy*. This may occur in solitary or loosely aggregated flowers, but is illustrated more generally by the outer florets of a relatively close inflorescence.

(iii). *Fusion* of parts, more particularly to form tubes. The most important type of fusion is sympetaly, which lies at the base of the primary division of Dicotyledons.

4. The "primitive flower," or prototype, will be, of course, one in which the working of these principles is realized the least. There will be no economy in production; the parts will be, therefore, produced in indefinite numbers; and there will be no great specialization for the reception of insect-visitors—no aggregation, chorisis, zygomorphy, or fusion of parts. An analogy to such a prototype is not wanting in the Gymnospermæ, for we find it in certain members of the Bennettiteæ, and reflected in the typical flowers of certain Ranalian orders, *e.g.*, the Magnoliaceæ.

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It is our purpose in the next chapter to illustrate the working of these principles, as briefly as possible, in the series Archichlamydeæ, and by this means to introduce the Sympetalæ, within which group an attempt will be made to trace the evolutionary progression in some detail.

(*to be continued*).

THE INTER-RELATIONSHIPS OF THE BRYOPHYTA,

By F. Cavers, D.Sc.

XI. RELATIONSHIPS OF BRYOPHYTA TO OTHER PHYLA.

IN the foregoing study of the morphology and inter-relationships of the Bryophyta, it has been assumed, as a working theory, that the Bryophyta, as arranged in the scheme of classification that has been outlined, in reality form an ascending series marked on the whole by progressive elaboration of the sporophyte; that the sporogonium of the Bryophyta has arisen as an interpolated generation, with gradually increasing "sterilisation of potentially sporogenous tissue," from the segmented oospore; that though the archaic condition in which the sporogonium was a simple spore-fruit, consisting of a mass of sporogenous cells enclosed in the venter of the fertilised archegonium, is not actually realised in any known Bryophyte, we have in the *Riccia* capsule a primitive sporophyte in which sterilisation has proceeded only as far as the formation of a single peripheral or epidermoid cell-layer constituting the capsule-wall; that the *Riccia* type of sporogonium is therefore not only the simplest but the most primitive known to us.

The view that the simple types of sporogonium found in *Riccia*, *Corsinia*, and the Sphærocarpales are not primitive, but *reduced*, would involve the assumption that extensive and far-reaching reduction has taken place in the evolution of the Bryophyta. Goebel has recently, in his memoir on *Monoselenium* to which reference has already been made, put forward the view that the Marchantiales constitute a descending series of reduction forms, starting from a *Marchantia*-like type, and that *Riccia* represents the lowest and most reduced member of this series. There can be no doubt that certain features in the morphology of *Monoselenium*, *Cyathodium*, *Monoclea*, and *Dumortiera*, all belonging to the Marchantiales, are best explained as reduction phenomena correlated with adaptation to moist and shaded habitats. As might be expected, the different organs exhibit different degrees of reduction. In *Monoclea* the thallus shows complete reduction of air-chamber tissue, along with almost entire abortion of the scales and tuberculate rhizoids characteristic of Marchantiales, but the sporogonium is highly developed, and instead of showing the slightest sign of reduction, differs from that of all other Marchantiales in having a long seta which raises the capsule well above the thallus and the substratum. In *Dumortiera* also, the sporogonium is apparently exempt from the reduction that has overtaken the gametophyte. In any case, however, it can hardly be maintained that the entire series of Marchantiales displays reduction caused by adaptation to moist or shaded habitats, for most of these plants are more or less decidedly xerophilous as compared with the Liverworts as a whole, and the markedly hygrophilous forms are pretty evenly distributed through the different divisions of the series.

It might be urged that reduction of the *Marchantia* sporogonium to the *Riccia* type has been caused by the hemming-in of the developing sporophyte by the tissues of the parent plant, leading to precocious formation of the spores and almost complete reduction of vegetative growth ; just as the germination of the spores of certain Ferns within the sporangium causes precocious formation of the sexual organs and reduction of the prothallus. If logically followed out, this view would have to be applied to the Bryophyta as a whole, and it would lead to the conclusion that the Bryophyte sporogonium was originally a free-living plant, which later became enclosed in the tissue of the gametophyte ; this retention might be supposed to have coincided with the evolution of the archegonium and with the passage from life in water to life on land, and therefore to have occurred in the algal ancestors of the Bryophyta. Many objections may be urged against this hemming-in or retention theory. To begin with, it may well be that the hemming-in of the *Riccia* sporogonium is the *effect* and not the cause of its simple structure, and that the *Riccia* sporogonium is embedded in the thallus because it has not developed the sterile basal tissue which enables the sporogonium of higher forms to raise its spore-producing upper portion above the thallus. Moreover, the well-developed sporogonia of the highest Marchantiales are hardly less embedded in the thallus than are those of such lowly types as *Corsinia*. The sporogonium of *Targionia*, which is sessile on the thallus, is quite as highly specialised as that of *Marchantia*, which is raised high above the thallus on the stalked carpocephalum.

The assumption that the simple structure of the *Riccia* sporogonium is primitive leads naturally to the conclusion that—whatever views may be held as to the relationship between the alternating generations in other phyla—the Bryophyte sporogonium had an antithetic origin, and that it has never been anything except a sporogonium. This tempts one to discuss the question whether the sporogonium may have given rise to the free-living sporophyte of the Vascular Plants. It has been suggested that the *Anthoceros* type of sporogonium forms a practicable starting point for the evolution of the Pteridophyta, but there are very great difficulties in the way of accepting such a hypothesis, which postulates the origin of roots and leaves from a sporogonium in the face of the fact that no known Bryophyte shows the slightest tendency to the development of such organs—unless, indeed, we may regard the foot of the typical Bryophyte sporogonium as a potential root, and the apophysis of Mosses like *Polytrichum* as a potential leaf.

If we adopt the view that the sporophyte generation originated as a free-living thallus, which later became hemmed in and retained in the parent plant, we are at once freed from these difficulties. However, it appears to the writer that the balance of evidence is distinctly in favour of the view that the Bryophyte sporogonium had an antithetic origin. In the general "pedigree table" on p. 40 indicating the writer's general conclusions regarding the interrelationships between the main groups of Bryophyta, expression is given to the suggestion made by Mr. Tansley that the "Archegoniate Algæ" from which the primitive Bryophytes arose also gave rise to the primitive Pteridophytes, because this appears preferable to the view that the Pteridophytes arose from the Anthocerotales or other highly differentiated Bryophytes.

The following list of literature merely indicates a few of the more important books and papers dealing with the subject; references will be found in these to other sources.

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A NEW SPECIES OF *DEBARYA*.

By S. Reginald Price, B.A.

[Plate II.]

SOME preserved material of a species of *Debarya*, which exhibited certain rather interesting features, recently came under notice I submitted a sample to Professor G. S. West, of Birmingham University, and he kindly informed me that it was a new species of the genus allied to *D. desmidioides*, West.[1]

The material had been fixed in chrom-acetic acid, and transferred to a dilute aqueous solution of glycerine which was allowed to concentrate by evaporation. The preservation was apparently quite good, so that the measurements (necessarily made on this fixed material) should only differ quite negligibly from those of fresh material.

The history of the sample is as follows. The sterile filaments, with other Algæ, were collected from stagnant ponds on Sheep's Green, Cambridge, by Mr. T. Elborn, and were transferred to the algal culture tubs kept outside the Cambridge Botany School. Conjugation took place here, and the material was fixed as already stated.

Diagnosis.

Debarya cruciata sp. nov. Filamentis longis, gracilibus, saepe dissociatis in cellulis singulis; cellulis vegetativis cylindricis, lateribus rectis, diametro 10-18 vel rarius 20-plo longioribus chromatophoris parvis, cum pyrenoidibus 3-7 in seriam unicam dispositis.

Conjugatio inter singulas cellulas post dissociationem filamentarum. Zygosporis rotundo-quadratis, lateribus levissime retusis, vel rarius convexis, angulis cornutis; cornibus cylindricis, solidis, apicibus rotundis.

Long. cell. veg.	60-140μ	lat. cell. veg.	6-8μ
Long. zygosp.	28-32μ	lat. zygosp.	20-24μ (sine cornibus);
Long. corn.	8-40μ	lat. corn.	8-12μ

The vegetative cells are remarkably delicate (probably the narrowest of the species described for Britain) and relatively long. The gametangia are always isolated single cells of the filaments, and separated vegetative cells are quite common. The chloroplast is relatively short and narrow and contains from three to seven pyrenoids, of which two or three are usually larger and more conspicuous than the rest.

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[1] West, G. S. Journal of Bot., 1903, p. 39.

The process of conjugation is very similar to that described for *D. desmidioides*, West[1] and *D. Hardyi*, West.[2]

The horns of the young "zygote" become filled by a deposit of cellulose as the gametes recede while at the same time the ends of the semi-gametangia round off. As the zygospore ripens these semi-gametangia apparently decrease in length, probably through the expansion of the conjugation canal.

The behaviour of the gametes can be followed for some time. As they recede into the conjugation-canal some of the pyrenoids decrease in size and become less distinct finally disappearing altogether, while two in each gamete enlarge and become more conspicuous. The gametes pass into the canal, as V-shaped masses with their apices directed towards one another. They may be seen lying side by side in the canal, the line of apposition being the short axis of the zygote. At later stages the two pyrenoids in each become still more distinct, and probably by this time all the others have disappeared; the fusing gametes therefore give the appearance of a four-armed cross, each segment of the cross containing one conspicuous pyrenoid. The walls of the "spore" now proceed to thicken considerably and become golden brown and highly refractive. The pyrenoids diminish in size and become indistinct; the cruciate arrangement of the contents persists, however, till a late stage, but finally disappears. The behaviour of the nuclei has not been followed, but it may be presumed that fertilisation takes place at about this stage.

A similar cruciate arrangement in the young "zygotes," is met with in those species of *Mougeotia* belonging to the section *Staurospermum* and in the Desmids *Cylindrocystis* and *Penium didymocarpum*.

In such species of *Debarya* as *D. Hardyi*, *D. desmidioides* and the one under consideration, it seems hardly correct to regard the whole contents of the gametangia as entering the zygospore[1] for the gametes as they recede deposit the cellulose thickenings of the semi-gametangia. The whole "zygospore" structure in the case of *Debarya* may, perhaps, be homologised with the so-called sporocarp of the Mesocarpaceæ. In each case cellulose is laid down by the gametes, probably before fusion of the nuclei has taken place, and the product of this final fusion—the true zygospore—surrounds itself by separate walls. In each case the true diploid spore is contained within a structure consisting of the gametangia, the conjugation canal and the cellulose deposits or walls laid down by the gametes.

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[1] L.c.

[2] West, G. S. Journ. Linn. Soc. Bot., 1907, XXXVIII, p. 104.

This species—*D. cruciata*, seems to exhibit a further point of comparison, for the behaviour of the gametes before fusion, corresponds to that occurring in the *Staurospermum*-section of *Mougestia*.

On the other hand, as West has pointed out,[2] *D. desmidioides* to which *D. cruciata* is related, may be regarded as indicating how the Desmidiaceæ have arisen from such forms, through *Cylindrocystis*. This latter is one of the Desmids which exhibits the cruciate appearance of the contents in its young "zygospore" stages. Thus it seems possible that *D. cruciata* indicates a relation between the genus *Debarya* and the Mesocarpaceæ on the one hand, and the Desmidiaceæ on the other.

Accordingly *Debarya* may be regarded as a form from which two lines of evolution diverge, the one leading to the Mesocarpaceæ and the other to the Desmidiaceæ. There still remains the bare possibility, however, that the Mesocarpaceæ gave rise to such forms as occur in the genus *Debarya*, and certain of these in turn led to the more primitive Desmids; in other words *Debarya* may represent a link in a somewhat retrograde line of evolution, leading from the Mesocarpaceæ to the Desmidiaceæ.

I should like to express my thanks to Professor West for examining the species, and to Mr. R. P. Gregory for his help and suggestions.

BOTANY SCHOOL, CAMBRIDGE. *March, 1911.*

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[1] Wille in Engler's Pflanzenfam. I, 2, p. 1.
[2] L.c. (1).

EXPLANATION OF PLATE II., ILLUSTRATING MR. S. R. PRICE'S PAPER ON "A NEW SPECIES OF *Debarya*."

All figures drawn with camera lucida—magnification 1,000 diam.

Fig. 1. Single cell of vegetative filament, showing chloroplast with five pyrenoids.

Fig. 2. Longer cell than that shown in Fig. 1. Relatively short chloroplast and seven pyrenoids.

Fig. 3. Early stage of conjugation. Each gamete contains two conspicuous pyrenoids, while the ends of the gametangia are becoming filled and highly refractive.

Fig. 4. Later stage shewing cruciate arrangement of the chloroplast in the conjugation canal. Fusion has not yet taken place, and the gametes lie side by side.

Fig. 5. Nearly mature zygote. The contents have laid down the walls of the "spore." The walls are brown and highly refractive. The cruciate arrangement can still be made out very faintly.

THE NUCLEUS AND HEREDITY.

By V. H. Blackman.

NÄGELI, in 1884, by the help of his theory of *idioplasm*, was the first to give precision to the discussion of the question of the mechanism of inheritance. In his "Mechanisch-physiologische Theorie der Abstammungslehre" he suggested that the two germ-cells both possess two kinds of protoplasm. One kind, which is possessed by them both in equal quantities, is the carrier of the hereditary qualities; while the other is present in abundance in the egg, but in the male cell occurs only to a minimal extent or may be absent altogether. The first he called *idioplasm*; the latter is the ordinary protoplasm concerned mainly with metabolic processes. This distinction of "plasms" in the sexual cells seemed to him to be the simplest explanation of the two facts, (1) that offspring as a whole resemble equally the two parents, (2) the great difference in bulk of the two sexual cells which is found in the higher plants and animals.

Nägeli's theory was only a speculation concerning a presumably invisible differentiation of protoplasm. In 1884, however, it was given a possible morphological basis by Oscar Hertwig and Strasburger. These two observers had been working on the phenomena of fertilisation in animals and plants respectively. As a result of their observations they were led, quite independently, to the view that the nucleus is the carrier of the hereditary properties, and that its substance, especially its chromatin, must be identified with the *idioplasm* of Nägeli. This view was soon accepted by many workers, such as Weismann, Kölliker, de Vries, Roux and Boveri, and proved itself a stimulating working hypothesis.

The grounds on which this view has won acceptance by so many biologists may be briefly summarised as follows. First, there is the equivalence of the nuclei of the male and female cells in fertilisation, shown in many cases by the fact that the two nuclei bring in equal number of chomosomes. Secondly we have the special phenomena of mitosis, in which the nuclear material is so carefully divided into, apparently, exactly equal and equivalent halves. Such a process does not seem intelligible unless it is conceived as a mechanism for the equal distribution, qualitatively and quantitatively, of the hereditary material. Thirdly we have the close relation of the processes of fertilisation and nuclear reduction.

Reduction seems to have no clear meaning apart from the prevention of the summation of hereditary material (possibly of organisation) which would be the result of consecutive processes of gametic union. A halving of the chromatin would seem to be quite unnecessary on ordinary physiological grounds, since the visible nuclear material may increase and decrease during the ordinary vegetative life of the cell. Fourthly there is the striking parallelism between the morphological phenomena of the reduction-division and the facts of Mendelian segregation. Fifthly we have the general phenomena of gametic union; for this process throughout the animal and vegetable kingdom, from the Protista to the highest animals and plants, is always characterized by a nuclear fusion, while the amount of cytoplasmic fusion varies greatly and *is sometimes reduced to zero.* The amount of protoplasm associated with the spermatozoon of animals is so small that it is of doubtful importance in heredity; it is most simply explained as mainly a motor-mechanism associated with the movement of the cell. In such forms as *Paramœcium* the two conjugating cells are united only by a narrow bridge of protoplasm, and while there is an obvious nuclear interchange there is no clear cytoplasmic interaction. Again in the case of such Angiosperms as *Lilium* and *Helianthus*, we have the observations (mostly neglected by zoologists) of Strasburger,[1] Nawaschin[2] and the writer,[3] which supply the critical evidence for the monopoly of the nucleus (at least in these cases) in the transmission of hereditary qualities. In these forms the *male element is in no sense a cell but is a mere, naked nucleus* of a spiral form and apparently self-motile.

To these five important lines of evidence may be added the contrast between the simplicity of the processes of cell-division and the complexity of ordinary nuclear division. This points to the superior importance of the nucleus, as does the fact that in many cases large portions of the protoplasm can be broken from the egg without interfering with its capacity to develop, after fertilisation, a a normal embryo. Again the first few cells of a developing egg may be shaken apart from one another and each will develop into a small complete embryo, though the amount of protoplasm with which each starts may be only one-eighth part of the original protoplasm of the egg. If there are in the protoplasm special carriers of the hereditary material, they must be repeated many times in

[1] Jahrb. f. wiss. Botan. Bd. 45, 1908.

[2] Oesterreichische Botan. Zeitschrift 1909, No. 12.

[3] Report of British Association, Sheffield 1910.

the egg so as to allow of a satisfactory distribution to all the eight portions.[1]

The hypothesis that the nucleus is of the chief importance in the transmission of hereditary properties, and possibly holds the monopoly in such transmission, is thus seen to be widely based on circumstantial evidence drawn from a variety of cytological phenomena, and it explains many processes which would otherwise be almost meaningless. It also fulfils the other test of a satisfactory working hypothesis, for it has certainly been productive of valuable results; in fact, we owe to its stimulus many of the most important investigations on cell-structure.

We may now turn to some of the criticisms which have been levelled at the hypothesis and we may consider first some of the more general objections.[2]

Verworn, Rabl, Fick and Conklin hold that there can be no such localization in the nucleus as has been hypothesized above, and that the cell as a whole must be the carrier of the hereditary properties. Conklin has spoken out very strongly against the Hertwig–Strasburger view. He says:—"Since heredity includes a series of fundamental vital processes such as assimilation, growth, division and differentiation there is something primitive and naive in the view that this most general process can be localized in one specific part of the cell—something which recalls the long-past doctrines that the life was located in the heart or in the blood, or the ancient attempt to find the seat of the soul in the pineal gland or in the ventricles of the brain."

The criticism seems really based on a misunderstanding, as Hertwig has pointed out. The hypothesis in question is not concerned with the metabolism of the cell or the processes of assimilation, growth, etc., but simply with the problem of the localization of a special function in a special part of the cell. Nucleus and cytoplasm are clearly of equal importance in the general life-processes of the cell. Without the protoplasm the "anlagen" carried, according to the hypothesis, by the nucleus would never be brought to development. As De Vries has pointed out, the transmission of a character and its development are quite different processes; the one may be the special function of the nucleus alone, the other the work of the cytoplasm or of the cytoplasm and nucleus together.

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[1] To these arguments may be added the definite association, shown by Wilson and others to exist in many insects, between the accessory chromosome and femaleness.

[2] Some of the points dealt with in this article are more fully discussed in O. Hertwig's "Der Kampf um Kernfragen der Entwickelungs- und Vererbungslehre," (pp. 1-122, Jena, 1909), and in C. Godlewski's "Das Vererbungsproblem im Lichte der Entwicklungsmechanik betrachtet," (pp. 1-301, Leipzig, 1909). The original references to papers quoted in this article have not been supplied when they can be obtained from these works. For the lower forms M. Hartmann's "Die Konstitution der Protistenkerne," (p. 1-54, Jena, 1911), may be consulted.

The second class of objections arise from those biologists who, like Verworn and Loeb, *deny to living organisms the possession of an underlying organisation* and consider plants and animals as mere complexes of materials reacting to chemical and physical forces. The question of the main distinction between dead and living material is of course one which in the present state of our knowledge it is not profitable to discuss at any length. It must be pointed out, however, that there is much to be said for the view, in no sense vitalistic, that the play of physical and chemical forces in the organism is regulated by a definite anatomical substratum. It is well known in chemistry that the reaction of a chemical substance depends largely on the configuration of the molecule, and recently the nature of crystals and such difficult questions as change of valency have been shown to be explicable on a theory of molecular architecture. It would seem possible then that the cell, or some smaller unit of it, is the seat of an architectural organisation on a higher scale, by means of which the activities and the form of the organism are controlled. Such a view is not a vitalistic one, for though the complexity of the living organisation is probably far greater than that of any dead material, yet it is possible that the one has arisen from the other, and that the living organisation has reached its present degree of complexity by slow degrees in long periods of time. If such an organisation be accepted the view is certainly tenable that there are material carriers of this organisation which are transmitted from cell to cell and are possibly localized in the nucleus.[1]

In relation to the third series of general objections, it is interesting to find that the attempt to explain such a process as development without having recourse to any fundamental organisation has led to the revival of the old theory of Sachs' of "organ-forming substances." This theory was put forward by Sachs in his article "Stoff und Form der Pflanzenorgane," as long ago as 1880. Sachs here contends that the morphological nature of an organ is dependent upon the material substance from which it is built up. On such a view there must occur in a plant as many specific formative materials as there are different organs: there would be specific materials for foliage leaves, scale leaves, bracts, floral leaves, root, stem, stamens, carpels, etc. Sachs' view obtained little support at the time, but of late years the theory of formative substances has been again brought forward by Conklin and Carl Rabl. They contend that the egg-protoplasm contains definite organ-forming substances which are necessary to development, so that the cytoplasm must be considered as a partner with the nucleus in transmitting hereditary properties. As Hertwig points out, the theory of these formative substances is such a vague one and so difficult to fit in with present-day biological conceptions that it can hardly be placed in serious opposition to the hypothesis of the nuclear idioplasm. It is not clear whether the substances are dead or living; they are certainly not present in all egg-cells, and they do not seem to enable us to explain the processes of regeneration. Even when such formative substances are present, as apparently in the eggs of Ctenophora, they can be considered as having arisen during the maturation of the egg as a result of the activities of the female nucleus.

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[1] It is difficult of course to understand how two organisations can fuse at fertilization, or if they remain separate then how they can mingle and be "reduced" at meiosis. Even on the view, which has found favour with some workers, that the factors which work in inheritance are of the nature of ferments there seems no objection to considering the nucleus as of chief importance in transmitting the mechanism for the production of these ferments.

Leaving the more general objections we may now review the chief objections to the theory on experimental and observational grounds. These fall mainly into two groups, those resulting from experiments on eggs and their fertilization, and those relating to the occurrence of simple amitotic divisions in plants and animals.

It was at first hoped that experiments on merogony (in which an enucleate portion of egg-protoplasm is fertilised by the spermatozoon of another species or genus) would provide a crucial test for settling the question. The earlier classical experiments of Boveri, in which fragments of the eggs of *Sphærechinus* were fertilised with the spermatozoa of *Echinus*, turned out later to be inconclusive. For though small larvæ were produced with purely paternal characters, it was shown that such forms might arise from normal hybrids of the two forms produced by fertilisation of a complete egg. Boveri's conclusion that the absence of the egg-nucleus was the cause of the absence of maternal characters could not then be accepted. Later, Godlewski (1906) made further observations on hybrid eggs of Echinoderms. He carefully sorted out the enucleate egg-fragments of *Echinus*, and found that on crossing them with the sperms of *Antedon* the larvæ showed in their young stages purely *maternal* characters, whether they arose from such fragments or from normal eggs. The merogonous larvæ unfortunately only lived a very short time, none of them proceeding beyond the gastrula stage, but the evidence certainly does show that, in some cases, the cytoplasm alone of the egg is able to impress upon the embryo, *at least in its early stages*, the purely maternal characters.

It is important, however, not to lay too much stress on these experiments, significant as they are. Godlewski himself does not claim that they in any way cast doubt upon the importance of the nucleus in the hereditary processes; all they do is to supply evidence that the protoplasm of the egg also plays a part in these processes. It must also be remembered, as already mentioned, that the protoplasm of the egg has been associated with the female nucleus during all the stages of maturation, so that at the time of fertilisation changes may have already been initiated in the egg (as the result of nuclear activity) which have already laid down the lines of early development. This would seem also to be the explanation of those cases in which removal of portions of egg-protoplasm cause deformity in the embryo resulting after fertilisation. The elegant experiments of Fischel (1897) may be mentioned, in which removal of different portions of the egg of *Beroë* caused different malformations in the embryos. There is no reason to doubt that these substances were produced under the influence of the female nucleus, nor is it surprising that in the absence of suitable materials to be activated certain organs should fail to develop even though the whole complement of hereditary properties is present in the nucleus.

Against the experiments of Godlewski we can set those of Herbst and Boveri. Herbst (1906-9) has made ingenious experiments on echinoderm eggs which were fertilised by a foreign sperm *after* they had been caused (by an artificial increase in the osmotic power of the surrounding medium) to start developing parthenogenetically. The start in the direction of parthenogenetic development led to an increase of the substance of the female nucleus relatively to that of the male nucleus, and it was found that in such eggs the development was shifted in the maternal direction, *i.e.*, the embryos were more like those of the female parent than they would have been if produced by a similar fertilisation of normal eggs. It certainly seems probable that these two facts are to be causally related.

The later work of Boveri (1907) again speaks strongly in favour of the importance of the nucleus in hereditary processes, and as the results are of particular interest they may be dealt with in some little detail. Boveri caused the eggs of Echinoderms to be fertilised by more than one spermatozoon. As a result of this the egg-nucleus does not divide regularly into two and then into four, but it proceeds directly to a multipolar, simultaneous division into three or four parts which are the nuclei of the first blastomeres. If now the first four blastomeres of such an egg are shaken apart, each will start developing independently into an embryo, but after a time these usually become abnormal. It is very interesting to note that the four embryos produced from the four blastomeres of a single egg often behave *quite differently*; some will carry their development much further than others and display quite different abnormalities. Complete eggs fertilised by two spermatozoa and allowed to develop show a normal development up to the gastrula stage, but in the later stages defects in the skeleton or some other part appear.[1] The striking point about these defects is that they are usually confined to one part of the embryo, that arising from one of the first three or four blastomeres.

The irregularity of distribution of the malformations Boveri explains by the irregularity of distribution of the chromosomes during the first multipolar division. If we take the case of *Strongylocentrotus lividus* there are eighteen chromosomes in the sexual cells; if such an egg is fertilised by two sperms it will have fifty-four chromosomes. When the egg divides, a spindle with four poles will be formed and the chromosomes may be distributed in the spindles as in Fig. A, where the dots represent

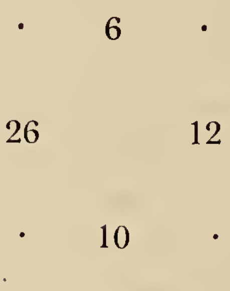

Fig. A.

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[1] The defects do not appear earlier because up to the gastrula stage the development of the egg is controlled by the egg-cytoplasm as shown in the experiments of Godlewski mentioned above.

the centrosomes of the asters of the quadripolar spindle. When the chromosomes split we shall have the arrangement shown in Fig. B. Two groups of chromosomes will meet in each blastomere and we shall finally have the four blastomeres with the number of chromosomes shown in Fig. C. Now the chromosomes are distributed on the spindle by chance, so that although each blastomere may have the number (eighteen at least) necessary for ordinary development, yet the qualitative nature of the various chromosomes meeting in a blastomere is a matter of accident.

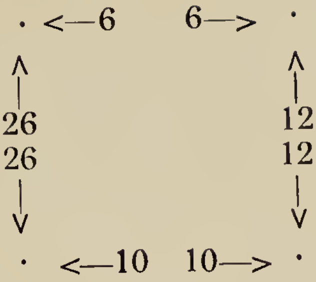

Fig. B.

32	18
36	22

Fig. C.

Boveri points out that the different behaviour of the different blastomeres cannot be explained on centrosome or protoplasmic differences, for the cytoplasm is distributed equally between the four cells; the difference must then depend on differences between the nuclei of the blastomeres. The abnormalities cannot be explained on the ground of the number of the chromosomes being too large or too small, for an examination of the size of the nuclei shows that malformations are found in embryos with neither abnormally large nor abnormally small nuclei. The abnormalities must thus depend on *qualitative* differences between the nuclei. The qualitative difference seems only to be explained by the general qualitative difference of the chromosomes of a single nucleus. In ordinary daughter-nuclei there is no qualitative difference, because each has a half of each of the *different* chromosomes of the mother-nucleus. In the particular type of division in question there is an irregular and chance distribution of the chromosomes, leading to qualitative differences between the four nuclei.

The interpretation then to be placed upon these experiments of Godlewski, Herbst and Boveri is that the nucleus is the controller of development as a whole, but the egg-protoplasm (probably owing to its activation by the female nucleus in earlier stages) is responsible in many cases for the first stages of embryonic development, which are thus purely maternal in character. There appears to be nothing in these observations against the view of the monopoly of the nucleus in the transmission of hereditary properties, a monopoly which certainly exists in *Lilium* where, as mentioned earlier, the fertilising element is not a cell but a naked nucleus.

When we come to consider the relation of amitosis to the hypothesis of nuclear idioplasm we are on much more difficult ground. The simple method of amitosis (in which the nucleus becomes drawn apart into two portions without any elaborate process of chromatin division) has been known for a long time, but until recently it has usually been held that amitosis was only to be found in cells which will soon degenerate, or at least was absent from cells in the direct line of the reproductive cells. Child and some other workers have described amitotic divisions in various tissues among the higher animals, even in connexion with the formation of the sexual cells, but the evidence brought forward has been sharply criticized and does not appear conclusive. Nuclear fusions are easily confused with amitotic divisions, and in order to prove that the nuclei produced amitotically are normal ones it is necessary that they should be followed later into an ordinary mitotic division which shows the *normal* number of chromosomes.

Among the lower plants the experiments of Nathansohn are the most conclusive. He treated *Spirogyra* filaments with a dilute solution of ether ,with the results that the nuclei divided amitotically. The cells so produced were isolated and grown under normal conditions, when they divided mitotically in a normal way. In the case of the lower fungi amitosis occurs without much doubt in such cases as *Synchytrium*,[1] *Spongospora*,[2] and *Plasmodiophora*,[3] and it seems also to occur in the Uredineæ.[4]

In the Protozoa also, direct amitotic division is frequently met with, though many forms show well-marked indirect (mitotic) division. Also in this group we meet with the fact that a fragment of a cell which contains only a *portion of the nucleus* may regenerate a complete new cell, as in the case of *Stentor*.

As to the relation of these facts of amitosis to the general theory of nuclear idioplasm it is impossible to say at present how much weight should be placed on evidence drawn from the lower forms of life. The question of the nature of the nuclei of the Protozoa is one of considerable complexity. One need only refer

[1] R. F. Griggs, Bot. Gaz. 47, 1909, p. 125.

[2] F. T. B. Osborn, Annals of Botany, XXV, 1911, p. 27.

[3] Prowazek, Arbeit. a. d. kais. Gesundheitsamte, XXII, p. 396.

[4] Blackman, Annals of Botany, 1894 ; British Association, Sheffield, 1910.

to the view that the nuclei of this group are not all comparable with one another; we have, in Hartmann's terminology, *monoenergid* and *polyenergid* nuclei, and we have mitoses of different nature. Again there is the hypothesis of the "dual" nature of the nuclei, which applies especially to the Flagellata, one part of the nucleus being concerned chiefly with the motor activities of the cell and the other being of ordinary, so-called idiochromatic, nature.[1] Also it appears possible that in many cases a protozoan nucleus is comparable not with the whole nuclei of higher organisms but merely with a single chromosome of such a nucleus. From such a point of view what appears to be a simple, *direct* nuclear division in a protozoon may be quite as efficient a process of equal division as that of the splitting of a chromosome of a nucleus of one of the higher forms. Then again there is the possibility that the material particles representing the simpler hereditary equipment of the lower forms may be many times repeated,[2] so that a less complex method of separation than that of mitosis with chromosome splitting may be sufficient to safeguard, during division, the equality of the hereditary equipment handed on to the new cells.

Some workers on the evidence of the occurrence of amitosis and the behaviour of the *Protozoa* have been inclined to give up the theory of the importance of the chromosomes and even that of nuclear idioplasm. This does not seem, however, a judicial position to take up on consideration of the balance of evidence from the two sides. On the one hand we have the evidence, of rather a doubtful nature, of amitoses in higher forms; and the evidence of amitoses in lower forms, which is rather difficult of interpretation. On the other hand there is the large amount of circumstantial evidence already detailed, the important experimental evidence of Godlewski, Herbst and Boveri, and the striking evidence from some of the Angiosperms. On the whole it must be admitted that, for the higher organisms at least, the theory of nuclear monopoly in the transmission of hereditary properties still holds the field, and is the theory which most fully explains the majority of facts. In the case of some Angiosperms the absence of the male cell-protoplasm may fairly be considered as direct proof of this monopoly.

[1] In the blood-parasite, *Hæmoproteus noctuæ*, for example, the sexually produced individual has a single nucleus which soon divides into two ,one an ordinary nucleus, the other, (the so-called blepharoplast) connected with the flagellum. On cell division both these nuclei can divide mitotically.

[2] This may explain the fact that the cell and nucleus of such a form as *Stentor* may be divided and each of the parts will grow into a complete individual.

XEROPHILY IN THE CONIFERÆ AND MICROPHYLLY.

THE xerophilous structure of the leaves of the Coniferæ has attracted much attention from the point of view of their ecological relationships. Since the leaf-structure is markedly xerophilous in respect of thickened cuticle, sunken stomata, etc., it has been customary to regard the whole tree or shrub bearing these leaves as a "xerophyte." The difficulty that has been found in correlating this structure with the occurrence of Conifers in situations in which apparently an abundant supply of water is available, has led to the tentative assumption that xerophily in these cases is a character fixed by heredity. For instance, Schimper,[1] speaking of the needles of the Larch, suggested that the slight relic in them of xerophilous structure must be regarded as hereditary, and of a character opposed to their present conditions of existence. Miss Stopes[2] also suggested that the xerophilous character of Conifer-leaves is due to the hereditary tracheidal structure of the wood, and the consequent limitation of the rate of flow of the water current. Professor Groom,[3] however, shewed that this explanation breaks down in the case of the Larch with its rapid transpiration current.

It is true that the assumption of the hereditary fixity of a character to explain apparent lack of adaptation may become merely an easy method of disguising ignorance of the real physiological relationships between a plant and its environment: this seems to be the case, to a certain extent, in the somewhat similar instance of "swamp xerophytes," where hereditary xerophily has been assumed by some authors. It is necessary in such cases to produce independent evidence of hereditary fixity, evidence unrelated to the supposed incompatibility of structure and habitat.

Let us therefore consider the Coniferæ from this point of view, with the object of discovering whether a strong hereditary factor enters into their powers of adaptation, and if so what may be its nature.

There is much disagreement as to the ecological adaptation of Conifers to their environment. On the one hand the assertion is

[1] Plant Geography (Engl. edition), p. 565, 1903.

[2] "The 'Xerophytic' Character of the Gymnosperms." New Phyt., VI., p. 46, 1907.

[3] "Remarks on the Oecology of Coniferæ." Ann. Bot., XXIV., p. 241, 1910.

made that the adaptation is imperfect. Schimper, for instance remarks (loc. cit. p. 564) " The xerophilous structure of Conifers is an hereditary character that does not always appear to correspond with the present conditions of existence of the Coniferæ. This statement, however, really concerns only certain places in the tropics, such as Java and Sumatra." Similarly, Miss Stopes (loc. cit.) considers that " frequently the marked protection of the Gymnosperms seems out of place and superfluous, as it appears in the lives of many species of *Abies*, the large American forest trees, and in the various species commonly found growing in a mixed deciduous forest." Schimper, however, denied that the Conifers are xerophilous. He observes: " It is by no means admissible to include them among xerophytes, as Warming has done. The term xerophyte may to a certain extent apply to several species of *Pinus* and *Juniperus* of dry sandy and stony soils, whose xerophily is determined by edaphic influences: but it does not apply to most species of *Abies* and *Picea*, our silver fir and spruce, for instance, which require as much moisture as broad-leaved trees, and are tropophilous in the whole of their mode of life." It may be observed that this is in part an argument from the conditions to the plants, and involves the assumption that the adaptation is perfect—an assumption contradicted by Schimper in the examples from Java and Sumatra (quoted above). Further, it would appear to be straining the term to call Conifers tropophytes, as Schimper does in respect of the young shoots, which " have only weak protective devices against transpiration."

On the other hand, Dr. Moss[1] goes to the other extreme, and speaks of " the undoubted xerophily of the Coniferales," which he regards as the character that has enabled these evergreen plants " to hold their own in the deciduous forests of the north temperate zone, and as being necessary for the continuance of the Conifers in a region, which, for more than half the year, is ecologically xerophytic." Similarly, Warming,[2] though contradicted by Schimper, maintained his former position, stating in a later publication that " the soil upon which coniferous forest occurs varies widely, yet, so far as reliable information is available, it is always physically or physiologically dry—a fact which harmonises with the xerophytic structure of Coniferæ. . . . . Miss Stopes is incorrect in assuming that Coniferæ nowadays do not for the most part grow under dry conditions of life."

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[1] " Xerophily and the Deciduous Habit." NEW PHYT., VI., p. 183, 1907.

[2] Oecology of Plants, p. 310, 1909.

There is thus considerable divergence of opinion on the subject, which seems to rest upon the lack of adequate evidence as to the exact habitat (in the narrow sense) of particular species, and as to their physiological powers. The difficulty of fixing criteria in matters of structure is also very acute here, as in other cases of adaptation.

The recent work of Professor Groom (loc. cit.), and his criticism and extension of von Höhnel's results in the estimation of the velocity of transpiration, have thrown much light on the subject. The most important result of this work is to shew that it is fallacious to judge of the xerophily of a plant from leaf-structure alone, and that a factor of fundamental importance is the total leaf-area. That this should have been so much neglected in the past is remarkable, but may perhaps be due to the prevailing tendency to base conclusions as to xerophily upon the examination of isolated leaves in the laboratory, without reference to the habit of the living plant. Clearly, to compare in this way, say, *Pinus sylvestris* with *Welwitschia mirabilis*, plants whose leaves shew quite similar xerophilous structure, can throw little light on the water-relations of the plants in nature.

Professor Groom considers that "the northern evergreen Coniferæ are '*architectural xerophytes*,' in which the extensive surface exposed by the evergreen leaves as a whole renders it necessary for the individual leaves to be xeromorphic in form and xerophytic in structure." He thinks it possible "that concurrent increases in the assimilatory surface and in the xerophytic devices generally increase assimilation in relation to transpiration" (an idea to some extent supported by the work of Renner[1] on the effects of sinking and narrowing of stomata); but that in the absence of statistics bearing on the subject "it is impossible to explain why the Conifers should have adopted the device of having a large aggregate surface with a greater degree of xerophytism."

Now the implication of the above quotations seems to be that the plant is extremely "plastic," and that in matters of adaptation it will always come to adopt that habit and structure which give the greatest degree of efficiency under the given environmental circumstances. In fact it is tacitly assumed that, had it been more advantageous to the Conifers to adopt the habit, say, of an oak-tree, they would not be found to-day to possess the characters that they actually do. A similar idea is expressed by Coulter & Chamberlain,[1] who consider that the development of the "small and rigid needles or concrescent scales" from their assumed broad-leaved ancestors "cannot be regarded as the result of a general tendency among Gymnosperms quite unrelated to conditions of living. . . . . The leaf is too variable a structure and too closely related in its work to external conditions to permit such an explanation of its changes."

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[1] "Beiträge zur Physik der Transpiration." Flora, vol. C., p. 451, 1910.

It appears that in the case of the Coniferæ this assumption may fairly be criticised. If the theory, advocated by Professor Seward, of the Lycopodiaceous origin of the Conifers be accepted, there is involved the conclusion that the small-leaved structure is primitive for the Conifers. If an analogy only be admitted between Conifers and Lycopods, this would appear to indicate that the small-leaved type is remarkably constant throughout large groups. Even admitting the megaphyllous origin of the Conifers, we are confronted with the fact that the same type of small-leaved Coniferæ has persisted from later Palæozoic times to the present day.

Moreover, there is much to be said in support of the view that, within the Conifers, the narrow one-nerved type of leaf is more primitive than the broader many-nerved type found in a few Araucarieæ and in *Podocarpus* § *Nageia*.

The evidence therefore seems to point to the conclusion that the small-leaved type is extremely stable: and this also seems to follow from what we know of modern Conifers. The variety in their habitat, though difficult to estimate, appears to be correlated with less variety in their structure, relations of leaves to stem, size of leaf, etc., than in the case of Angiosperms. The Larch, with its deciduous habit and lesser degree of structural protection against transpiration, but with its retention of the microphyllous foliage, is a striking example of the persistence of what we have come to regard as the typically Coniferous form of leaf. Moreover, the deciduous species of *Taxodium* and *Glyptostrobus* inhabit swampy situations without modification of the type of leaf-form. In *Phyllocladus* the plant has even resorted to the device of producing flattened shoot-expansions in place of increasing the size of its leaves: and the same is the case in Hollick & Jeffrey's new Cretaceous Conifer, *Androvettia statenensis*, which they refer, on anatomical grounds, to the Araucarineæ.[2]

[1] Morphology of Gymnosperms, p. 413, 1910.

[2] Studies of Cretaceous Coniferous Remains from Kreischerville. New York, 1909, p. 22.

It seems, then, that emphasis should be laid on the small power of the Conifers to vary the character of their leaves. The predominant types—*viz.*, the acicular leaves of *Pinus*, *Abies*, *Larix*, etc., the linear-lanceolate leaves of *Taxus*, *Cunninghamia*, etc., the scale-like appressed and "concrescent" leaves of *Cupressus*, *Libocedrus*, etc.—are all closely related to one another. The development is in all cases small compared with that of the stem: *i.e.*, the Conifers are in fact fixedly microphyllous, whatever they may be according to phylogenetic theory.

This prevalence of the narrow acicular, linear-lanceolate, and cupressoid types of leaf seems to be connected with the absence of lateral pinnation of the foliar vascular system. In the majority of cases a single or double median vascular strand runs from end to end of the leaf without branching: and even in the § *Nageia* of *Podocarpus* and certain Araucarieæ where the leaf is broader and many-nerved, there is not found that copious lateral branching and anastomosing of the veins with which the free pinnation of the leaves of so many Dicotyledons is associated.

The failure of the bundles to branch is compensated to some extent by the development of transfusion tissue; as in the case of certain fossil Lycopods, in which group the same limitation of the power of branching, microphylly, and sometimes xerophilous structure, seems to obtain.

Thus it appears that the Conifers are rigidly microphyllous forms, and that the power of freely adapting themselves to ecological conditions is strictly limited by the lack of plasticity in leaf structure. It is suggested that the lack of ability of the foliar vascular system to branch with ease is one of the causes which have contributed to keeping the leaf small: and that this failure may possibly be associated with the presence of transfusion tissue, which, though valuable in itself under the circumstances, may conceivably tend to prevent improvement in other directions, such as that of free pinnation of the vascular strands.

Given this cramped hereditary type of structure, ecological adaptation appears to have been the result of two processes going on simultaneously: (1) the development of enormous numbers of the rigidly constructed leaves with a view to increased assimilation and growth, and (2) the production of xerophily in the individual leaves as a compensation for the resulting increase of surface.

It thus seems clear that the hereditary factor is of great importance in the ecological relationships of the Coniferæ. It is conceivable that ecological adaptation may be achieved as efficiently by a suitable modification of the small-leaved type as by another kind of modification of a broad-leaved type: in fact, more than one kind of mechanism may be well adapted to a given set of external conditions. The Conifers are, however, predisposed to the adoption of "architectural xerophily" as their mode of adaptation by the persistent hereditary factor of microphylly.

R. H. COMPTON.

Cambridge,
March, 1911.

ON A METHOD OF SEALING UP THE COVER-GLASSES OF PREPARATIONS MOUNTED IN GLYCERINE.

[TEXT-FIG. 15].

DURING a recent visit of Professor Nathorst to Cambridge, he brought to my notice a method of sealing up slides in which glycerine was used as the mountant. The method has proved so useful that it ought to be more widely known. It consists in the application of hot wax to edges of the cover-glass by means of a piece of thick copper wire.

The wax was invented by Professor Lagerhein and described by him in the "Botaniska Notiser" for 1902.[1] It consists of hard paraffin wax (M.P. 55°-60°C) and mastic in equal parts. The mastic is powdered and cautiously heated in a porcelain dish until melted, when the paraffin is added in small pieces and the mixture stirred with a piece of wood until homogenous and free from lumps. It is then poured out into a flat dish (*e.g.* a Petri-dish) and when cool is ready for use. If desired, it may be coloured by the addition of some dye which will not be dissolved by the glycerine, such as Grübler's "Buttergelb."

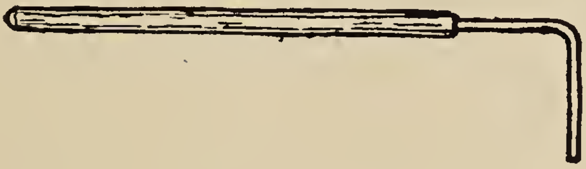

Fig. 15.

The wax is applied by means of a thick copper wire, one end of which is fixed in a wooden handle, while the other is straightened and bent at right angles so as to give a straight piece just a little longer than the length of the cover-glasses used (see Fig. 15). The straight portion is now heated in the flame of a Bunsen burner, dipped into the wax and gently applied, so that the wax-covered wire lies along the edge of the coverslip, from which superfluous glycerine should have been previously removed. The melted wax which adheres to the wire at once solidifies where it touches the glass and forms a neat and strongly adhesive joint. After each edge has been sealed and any superfluous wax scraped off with a knife, the slide is ready for use. The line of wax should adhere to the clean and dry portions of the glass at least along its inner and outer edges. If the specimens are to be kept for some time, a thin coating of gold-size may be painted over the wax.

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[1] G. Lagerheim. Metoder för pollenundersökning, p. 75.

The method has several advantages. The slides may be sealed up very quickly and used at once. The wax never percolates under the coverslip, as Gold Size and Brunswick Black often do. The coverslip can be easily removed with a knife, if at any time it is desired to restain or remount the section.

I am indebted to Professor Nathorst for the above particulars.

H. H. T.

NOTES ON RECENT LITERATURE.

Iron-Bacteria.

THE existence of bacteria which have the power to live in absence of organic foods was established by Winogradsky's well known classical researches on the nitrifying bacteria. These organisms proved not only to require no organic carbon in the nutrient medium on which they were cultivated, but to be injured by the presence of organic compounds even in very small concentrations.

A few years before this discovery, Winogradsky had investigated a species of another group of bacteria, the iron-bacteria, and his observations suggest a similar conclusion with regard to this organism. *Leptothrix ochracea* is a filamentous bacterium enclosed in a gelatinous sheath. In presence of this bacterium ferrous carbonate is oxidised and a precipitate of ferric hydrate accumulates in the sheath. For this precipitation, as also for the life of the organism, free oxygen is essential. Under the conditions prevailing in Winogradsky's cultures *Leptothrix* only grew when supplied with ferrous carbonate, and it was concluded that the oxidation of iron played an essential part in the metabolism of the bacterium.

Winogradsky did not follow up this first preliminary investigation with more critical experiments. Meanwhile Molisch found that *Leptothrix ochracea* could store manganese in place of iron, and succeeded also in cultivating the same species in organic nutrient media in the entire absence of iron and manganese. In opposition to Winogradsky's view he maintained that the oxidation and accumulation of iron do not depend upon the activity of the organism and are not essential to it: a similar accumulation was shewn to take place by adsorption and chemical oxidation in the sheaths of dead cells. He supposed that *Leptothrix* is merely heterotrophic and that in Winogradsky's cultures the minute traces of organic impurities were sufficient for its needs.

This seems extremely improbable as an explanation of Winogradsky's results, and it has been suggested (see Czapek, Biochemie II., p. 413) that Winogradsky and Molisch were working with two distinct forms. Recent work by Rudolf Lieske, however, provides an alternative explanation, since it confirms or affords parallel observations to the main results of both.

Lieske worked more especially with *Spirophyllum ferrugineum*, which forms flattened twisted filaments without any gelatinous sheath, and accumulates iron uniformly in the interior of the cell. He was quite unsuccessful in his attempts to cultivate this organism in organic nutrient media, or by any of the methods previously used for other forms. His later experiments showed that sugar, asparagin, and peptone, substances which provide excellent bases for the nutrition of most bacteria, inhibit the growth of *Spirophyllum* even in very small concentrations. By the careful exclusion of all organic impurities he was able to prove that it can flourish in the entire absence of organic nutrient substances, so long as it is supplied with ferrous carbonate.

He arrived at a suitable method of culture by closely imitating the conditions under which he found *Spirophyllum* growing in nature. The culture fluid contained the necessary mineral salts, iron was supplied in the form of coarse filings, and the open vessel was enclosed beneath a bell-glass with air enriched with about 1% of CO_2. Under these conditions sufficient iron was dissolved by the CO_2 in the water to enable the organism to develop luxuriantly. (According to Lieske's observations water always contains a high percentage of CO_2 where iron-bacteria flourish.)

Light proved to be without effect on *Spirophyllum*. Outside the laboratory it flourishes equally well in closed water-pipes and in iron springs. Oxidation of iron is therefore the only apparent source of its vital energy. Other iron salts than ferrous carbonate, and salts of manganese and other metals were tried without success; only ferrous carbonate itself, or iron or ferrous sulphide in presence of CO_2 (*i.e.* an indirect supply of ferrous cabonate) gave in Liekske's experience any development of *Spirophyllum*.

These results are obviously inconsistent with the view that the precipitation of iron is here purely a physico-chemical phenomenon. Subsequent experiments with gelatine, hardened in formaline, and the observation of dead filaments, showed that far more iron is accumulated by the living *Spirophyllum* than by dead adsorptive substances. The iron reaction is never so intense in the latter and they adsorb all compounds alike. Moreover the precipitation of ferric hydrate is an equilibrium phenomenon, the reverse reaction taking place in presence of an excess of CO_2: nevertheless, *Spirophyllum* continues to accumulate iron even under these conditions.

For *Spirophyllum*, then, it seems to be definitely proved that the accumulation of iron in large quantities is bound up with the vital activity of the organism. As has been already mentioned, Winogradsky held the same view with regard to *Leptothrix ochracea.* He observed that the gelatinous sheath which surrounds the filaments in this form continued to accumulate iron only where it enclosed a living cell; and as his culture fluid contained only minute traces of organic substances it seemed unlikely that these would be sufficient for the organism apart from the energy obtained by active oxidation of iron. Lieske has repeated Winogradsky's culture experiments and confirms his main results. As he found *Leptothrix* growing in nature in water in which he could detect no organic material he is inclined to the view that *Leptothrix*, like *Spirophyllum*, *can* live autotrophically, in absence of organic nutrient substances, by the oxidation of iron. On the other hand he was able, like Molisch, to cultivate the same species on peptone-gelatine media containing manganese, but no iron. Molisch succeeded further in cultivating it on organic media without either iron or manganese. This form thus differs from *Spirophyllum* in being able, apparently, to live either heterotrophically or autotrophically. How far *Leptothrix* makes use of its heterotrophic capabilities in nature is uncertain: Lieske never found either this or any other iron bacterium in iron springs with a high organic content.

No evidence is available as to the precise way in which the oxidation of ferrous carbonate is effected or how the energy so liberated is utilised. Whether the carbon required for the growth of the organism is obtained direct from ferrous carbonate or as free CO_2 can scarcely be determined. CO_2 could not be assimilated in absence of iron for want of the necessary energy; and it is impossible to supply ferrous carbonate without at the same time supplying free CO_2, for ferrous carbonate in solution undergoes hydrolytic dissociation. Quantitative experiments, too, present difficulties which Lieske has not been able to overcome.

Finally, Lieske's observations and experiments throw an interesting light on the biology of iron-bacteria. The occurrence of the different forms is affected by temperature as well as by the presence of iron. *Spirophyllum* flourishes even at 0°C, in brooks partly covered with ice, and grows most luxuriantly at 6°. At 22° on the other hand little growth occurs, and at 27° it ceases altogether to develop. In consequence of this Lieske was unable to find any trace of *Spirophyllum* in the warm summer months. *Leptothrix* is to be found growing well at all seasons of the year, and temperature seems to affect its rate of growth but little; while other forms (*Clonothrix*, *Crenothrix*) grow best when the water is warmest (18—25°C), disappearing altogether when the cooler weather approaches.

D. T.

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FLORAL EVOLUTION; WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

BY H. F. WERNHAM.

II. THE ARCHICHLAMYDEÆ, AND THEIR PHYLOGENETIC RELATIONS TO THE SYMPETALÆ.

IT is a remarkable fact that, whereas the flowers of barely 20% of the total number of species of Archichlamydeæ have stamens equal in number to, or less than, the corolla segments, an isomerous or oligomerous andrœcium characterizes nearly 95% of the species of Sympetalæ. Only about 18%, again, of the Archichlamydeæ have a pistil composed of two syncarpous carpels or, in some rare cases, of one only; in the Sympetalæ, on the other hand, fully 75% of the species have flowers with a bicarpellary gynæcium.

The natural conclusion to be drawn from these facts is that the progressive tendency to economy of production, observable at work, so to speak, in the Archichlamydeæ, has reached a high degree of realization in the Sympetalæ. In accordance with the principles formulated in the first chapter, we shall consequently expect to find, in the latter group, the second fundamental principle, that of progressive adaptation to insect visits, the more active. This is actually the case; a corolla-tube, of course, is almost invariably present in the Sympetalæ; aggregation into dense inflorescences is the principal feature of the Compositæ, which comprise over 27% of the total number of sympetalous species, and, indeed, over 10% of the sum total of flowering plant-species. Zygomorphy, moreover, occurs in quite 45% of the Sympetalæ, as against barely 15% in the case of Archichlamydeæ.

There seems to be little room for doubt, then, that, taken as a whole, the Archichlamydeæ are relatively primitive, while the Sympetalæ are relatively advanced, the cohesion of the petals going hand in hand with general oligomery on the one hand, and progressive adaptation to insect visits on the other.

With this introduction, we may proceed to trace the working of the evolutionary tendencies through the series Archichlamydeæ, and attempt, by this means, to find some phyletic connection between this group and the Sympetalæ.

Engler has divided the Archichlamydeæ into the following cohorts:—

(*a.*) Verticillatæ, Piperales, Salicales, Myricales, Balanopsidales, Leitneriales, Juglandales, Fagales, Urticales, Proteales, Santalales, Aristolochiales, Polygonales, Centrospermæ.

(*b.*) Ranales, Rhœadales, Sarraceniales, Rosales, Geraniales, Sapindales, Rhamnales, Malvales, Parietales, Opuntiales, Thymelæales, Myrtifloræ, Umbellifloræ.

The letters (*a*), (*b*), are our own; the first group (*a*) coincides approximately with the Incompletæ of Bentham and Hooker; and the second (*b*) includes those forms which these authors have named Polypetalæ, with the exception of the Thymelæales, which fall under the head of Incompletæ in the older system.

It will be convenient to examine first the essential organs in order.

1. *The Andrœcium.* In group (*a*) the number of stamens shews a wide range of variability, but a distinct tendency to oligomery is observable within the limits of each of the cohorts included in Amentaceæ,[1] and the Piperales.

The transitional arrangement $A = P + P$ prevails in Aristolochiales, Polygonales, and Centrospermæ—P denoting the number of perianth segments.

Isomery of the andrœcium is a fixed character of Urticales, Proteales, and Santalales, and it occurs also in a good many of the Centrospermæ and Polygonales. The stamens in these cases are however, usually inserted opposite the perianth segments,—and this is significant for our purpose as suggesting the probable abortion of an outer alternating whorl.

A decided tendency to indefiniteness in numbers—here

[1] The term Amentaceæ is used here to cover the cohorts Salicales, Myricales, Balanopsidales, Leitneriales, Juglandales, and Fagales.

regarded as secondary[1]—is a feature of the cohorts Aristolochiales and Centrospermæ.

Group (*b*) displays clearly the progressive tendency to oligomery. The primitively indefinite number of stamens which characterizes so many Ranales is comparatively rare in other cohorts; we meet it in a few of the Rosales, in the Sarraceniales, and possibly in a few of the Rhœadales; although a dominant note in the latter cohort appears to be secondary branching, and the indefinite number of stamens found in many Papaveraceæ, Capparidaceæ, etc., may be secondary, the result of active chorisis. The branched stamens in the Fumarieæ are suggestive in this connection.

The arrangement A=C+C, where C denotes the number of corolla segments, is attained in a few members of the Ranales, Rhœadales, and Sarraceniales; it prevails in Rosales, Geraniales, groups B and D of Sapindales, and in Thymelæales.

The condition of isomery, A=C (or less than C in some cases), is reached with decreasing rarity as we proceed along the line Ranales, Sarraceniales, Rosales, Geraniales, Sapindales (groups B, D), and Thymelæales; it occurs also in some Parietales; it prevails in groups C and E of Sapindales, and in Myrtifloræ; and it is a constant character of Rhamnales, in which the stamens are opposite the corolla-segments, and of Umbellifloræ, where they alternate with them.

The Umbellifloræ may thus be regarded as standing at the head of the Archichlamydeæ in relation to isomery of the andrœcium, for here isomery is a fixed character, and the alternation of the staminal whorl with the corolla segments leaves no suggestion of an ancestral second whorl.

The cohorts Rhœadales, Malvales, Parietales, Myrtifloræ, and Opuntiales are here regarded as expressive of the tendency to chorisis, of which the Opuntiales are the highest expression.

Cohesion of stamens, to a greater or less extent, characterizes most of the natural orders in Geraniales (groups A, B, C), Malvales, and Parietales (group A).

2. *The Gynæcium.* In group (*a*), and in certain so-called "anomalous" orders, the prevailing number of carpels is 2, *e.g.*,—Verticillatæ (Casuarinaceæ), Salicales, Myricales, Balanopsidales, Juglandales; also Podostemaceæ and Callitrichaceæ.

A tendency to reduction appears in Piperales (4 to 1), and Urticales (2 to 1); while in Leitneriales, and the highly specialized Proteales, a monocarpellary gynæcium is a constant feature.

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[1] *Supra*, p. 80.

For the rest, the number of carpels varies, but 3 or 3*m* is a common number,—Fagales (3–2–6), Santalales (3–2-1), Aristolochiales (6–4–1), Polygonales (3), Centrospermæ (3–1–5–∞).

Proceeding to group (*b*), a primitively indefinite number of carpels occurs prevailingly in Ranales, and in certain Rosales; the large numbers found among Parietales, Malvales, Myrtifloræ, and Opuntiales, may be, as in the case of the andrœcium, the result of chorisis.

The condition G=C prevails in Rosales, and in Geraniales (groups A, B).

The transition from G=C to G=2 is observable in a few Rosales, in groups C and F of Geraniales, in Rhamnales, and Thymelæales, G=3 being a common number. A tricarpellary ovary occurs frequently in Sapindales, in which cohort the carpels are rarely so many in number as the petals, although G=2 is not uncommon.

Of the Umbellifloræ, the Araliaceæ retain the arrangement G=C; but the remaining members of this cohort, including the large order Umbelliferæ, have a bicarpellary gynæcium.

It will be gathered from these statements that the gynæcium displays a development parallel with that of the andrœcium so far as numbers go, both in progressive oligomery and in secondary branching. The general tendency, moreover, is to a pistil of 2 carpels, 3 being perhaps the number of most common occurrence in the Archichlamydeæ; this may very probably be the result largely of mechanical causes.

In respect to fusion of the sporophylls, however, the evolutionary development of the gynæcium is far ahead of, and quite independent of, the development of the andrœcium. An apocarpous pistil is decidedly the exception in the Archichlamydeæ, and is non-existent —primitively at any rate—in the Sympetalæ. This is readily intelligible on the grounds of mechanical conditions of growth and economy of space, the female portion occupying the central position in the flower, and also in view of a general tendency, to be mentioned presently, to form a unilocular ovary, frequently containing a single ovule only.

In group (*a*) syncarpy is the rule, with very rare exceptions, and the ovary is nearly always unilocular.

Of group (*b*) Ranales is the only cohort which is characterized by an apocarpous pistil, and true apocarpy is extremely rare in the other groups. It is found in the Rosales; while the transition to syncarpy is traceable in Geraniales, in which cohort every gradation from relatively slight to complete union of the carpels may be observed from a comparative study of the natural orders and genera.

A tendency to the unilocular condition of the ovary is seen in the series Rosales, Geraniales, Sapindales, Rhamnales, Malvales, Parietales (group A),[1] and Myrtifloræ, in which, although the number of loculi usually equals the number of carpels, examples of a one-chambered ovary occur with greater or less frequency. In the remaining groups of Parietales, in Opuntiales, and in Thymelæales, the ovary is prevailingly unilocular.

In Myrtifloræ and Umbellifloræ, the number of loculi equals the number of carpels; so that, in the Archichlamydeæ, the tendency to economy as expressed by a unilocular and uniovulate ovary is not so powerful as to find reflection in its highest groups. We shall find in the Sympetalæ, however, that this tendency is much more clearly defined.

Progressive reduction in the number of ovules is to be expected, in accordance with the principle of economy in production; but this tendency is, we shall find, not so marked as the tendency to oligomery of sporophylls. We may suggest that the "effort" to produce an ovule is far less than the effort to produce a sporophyll; and, in many cases, prodigality in ovule production is counterbalanced in the course of seed-production, many of the ovules, or even all save one, being aborted at a comparatively early stage of development.

In the flowers of group (*a*) one or two ovules only are present as a general rule, the exceptions being found in Salicales, Proteales, Aristolochiales, and some Centrospermæ, in which groups the ovary is multiovulate.

Of group (*b*) Rhæadales, Sarraceniales, Rosales, Malvales, Parietales, Opuntiales, Myrtifloræ, usually have an indefinite number of ovules in the ovary; while 2 or 1 (per loculus) is the usual number of ovules in Geraniales, Sapindales, Rhamnales, and Thymelæales. These latter are the groups, it is pointed out, in which no general tendency to secondary branching has been noticed.

In Umbellifloræ the climax of economy is reached in the invariable production of one ovule only for each carpel.

We gather from the foregoing summary of the Archichlamydeæ that there is an unmistakeable tendency to economy in production of parts, particularly of sporophylls, but less markedly, perhaps, of sporangia.

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[1] Includes principally the *Guttiferales* of Bentham and Hooker.

The question arises, to what extent has the working of this principle of economy been accompanied by the compensatory tendency of progressive adaptation to insect-visits?

(i.) As regards progressively increasing *conspicuousness*, there is no strong general tendency to floral aggregation such as we find realized and expressed in the Compositæ. Dense inflorescences, close capitula of florets even, are found—and not very uncommonly—in isolated cases throughout the Archichlamydeæ; but aggregation does not characterize any relatively large group, save one,—the Umbelliforæ,—in which the inflorescence unit is typically a close umbel, often delimited, like the Composite head, by an involucre of bracts. The constancy of this feature in so large a group is significant when we couple it with the advanced state of its flowers from the point of view of the economy principle—their isomerous alternating whorl of stamens, and their bicarpellary gynæcium.

We may remark, moreover, that although the Umbellifloræ thus stand apart from and ahead of the other groups of Archichlamydeæ in this character of aggregation, it is not impossible that the efforts, so to speak, of the tendency to aggregation by active branching of the floral axes, are reflected in those relatively high groups,[1] of varying affinity and comprising a large number of species, in which, we have suggested, chorisis has occurred in the parts of the individual flower, producing indefiniteness in some or all of them.

(ii.) The general tendency to *zygomorphy* goes hand in hand with the progressive aggregation noticed above, the outer florets of the inflorescence tending to bilateral symmetry; this displays itself most conspicuously in the increased development of the corolla on the outer side, the result being comparable with the development of "ray" florets in Compositæ; and, as in the latter case, the outer florets in certain Umbelliferæ may become unisexual.

As we have already observed, this type of zygomorphy is probably the direct result of the mechanical conditions of development, growth in the corollas of the outer florets being directed, by the stimulus of pressure, towards the exterior.

As regards the other "type" of zygomorphy,[2] which appears in relatively large and solitary flowers, there is no general tendency to this condition in the Archichlamydeæ. Like the capitulate inflorescence, zygomorphy is not very uncommon in particular and phyletically isolated cases from among the Ranales upwards; but it does not form a critical character of any synthetic group comparable with the Lamiales and Personales of Bentham and Hooker—with which we shall have to deal later.

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[1] *Supra*, p. 80.

[2] *Supra*, p. 81.

Zygomorphy occurs in the following groups of Archichlamydeæ:

Proteales (Proteaceæ), where it is prevalent; Santalales, Aristolochiales, Rhœadales, Opuntiales,—where it is not uncommon; it characterizes many members of groups D and E of Geraniales, and D and E of Sapindales; while examples of zygomorphy are not lacking in Ranales, Rosales (notably the Papilionatæ tribe of Leguminosæ), Parietales, and Myrtifloræ.

All these cases, however, together with the Umbelliferæ, amount to about 15% of the total number of species of Archichlamydeæ.

(iii.) *Fusion*, in so far as this tendency subserves the principle of progressive adaptation to insect-visits, plays a very inconspicuous part among Archichlamydeæ. A corolla-tube is, of course, characteristically absent; although one or two specialized "apetalous" groups, notably the Proteales, the Aristolochiales, the Nyctaginaceæ, etc., have flowers with a typically gamophyllous perianth. In a few rare cases, too, a gamopetalous corolla occurs among the higher heterochlamydeous forms; but in the majority of these it would appear probable that the cohesion occurs some time after the initial stages in the development of separate petals have been passed. It may be suggested, perhaps, that a truly sympetalous corolla would seem to be one in which the component petals are united, if not from the outset of development, then at a very early stage. One result of such a circumstance would be that a pseudo-sympetalous corolla, if we may so express it, would conceivably betray itself by the absence of close cohesion at the base: and this is actually the case in *Correa*, for example, an Australian Rutaceous plant cultivated occasionally in conservatories. In some species of *Correa*, moreover, the corolla-tube breaks up after maturity into separate petals.

A tendency to tube-formation by cohesion of the staminal filaments is clearly distinguishable in the Geraniales; for in most of the natural orders of this cohort the filaments are more or less united, at least at the base. This tendency reaches its highest expression in the Meliaceæ, a large tropical and sub-tropical order, in which the anthers are typically sessile about the mouth of a tube composed of the united filaments. A staminal tube, again, is a familiar feature of the Papilionatæ.

The consideration of tube-formation leads us to make a necessary digression from the subject of fusion, to a tube-forming tendency among the Archichlamydeæ which is far more extensive than those already mentioned—namely, by means of the progressive hollowing of the floral receptacle. This finds expression in the so-called "calycifloral" arrangement; and this, apart from its relation to insect-adaptation in virtue of the consequent formation of a tube, reverts in its significance to the primary principle of economy in production; for it permits of the coalescence of carpellary with receptacular tissue, and material is obviously economized as the result.

The progressive hollowing of the thalamus is foreshadowed even in the Ranales, of which the Calycanthaceæ and Monimiaceæ have "perigynous" flowers. Perigyny is a critical character of the Rosales; and the series of rosaceous types illustrative of the progression from hypogyny to extreme perigyny tantamount to epigyny, is familiar to all. The Geraniales and Sapindales—the "Disciflorae" of Bentham and Hooker—have escaped this tendency, although the Celastraceæ reveal a certain leaning to epigyny by the sinking of the carpels in the flattened receptacle. The Thymelæales afford an excellent illustration of an intermediate stage in the calycifloral process; for here the receptacle is hollowed into a long tube, the frequent colouring of which displays its relation to insect visits; but the ovary remains free, as a rule, at the base of this tube. In Rhamnales a similar arrangement obtains, but the ovary is in this case usually united with the receptacular wall.

The final stage is seen in, *e.g.*, group C of Parietales, in Myrtifloræ and in Opuntiales, in which the ovary is completely sunk in the axis and united with it, *i.e.*, is inferior. Engler's division of his cohort Parietales is instructive in this connection; in group A the pistil is free, upon a convex axis; in B, the pistil may be situated in a tubular axis, but is rarely united with it; while in C, which includes the Begoniaceæ, the ovary is inferior.

It will be convenient to suggest at this juncture that inferiority of the ovary may, not improbably, have been produced in descent in more than the one way we have indicated, although this latter is alone in having left any continuous trace among existing plants. The point that we wish to urge here is, that, whatever the evolutionary methods of its production may have been, the inferior position of the ovary conduces to economy in production, since, in virtue of this position, receptacular tissue can be pressed into the service of ovule-protection and of fruit-formation. In any case it is certain that those floral types, such as the Compositæ, which are admittedly in the van of evolutionary advancement, invariably possess an inferior ovary, while no epigynous flower can be called unquestionably primitive.

We are now in a position to approach a study of the Sympetalæ. The sole essential difference between the Archichlamydeæ and the Sympetalæ is that the corolla in the latter group is composed of united petals, while in the former the petals are free.

We have attempted to portray the significance of this cohesion; its essence, in a word, is adaptation to insect-visits; and the formation of a corolla "tube" is at once the most elementary and the most extensively occurring structural device to this end.

Now it is not to be supposed that this cohesion of petals followed upon one evolutionary line of descent only; nor, further, that sympetaly originated at one point only—the terminal point—of any particular line. Thus, one main line in the Archichlamydeæ is determined by the principle of economy in the production of parts, traceable, first, in the reduction of the stamens to two whorls with obdiplostemonous arrangement, and, secondly, in the further reduction to one isomerous whorl, the corresponding members of corolla and andrœcium being placed, primarily, each opposite to the other, and secondarily, in an alternating arrangement. It is not reasonably to be anticipated that the tendency of progressive adaptation to insect visits would lag so far behind the principle of economy as to wait, if we may so express it, until an isomerous andrœcium was established before it produced a sympetalous corolla. Nor, indeed, is such the case; the *Heteromeræ*, one of Bentham and Hooker's three main divisions of the sympetalous Dicotyledons (corresponding to the *Pentacyclidæ* of Engler), reflect the association of a sympetalous corolla with a double staminal whorl. In the Primulales, the stage at which the stamens are equal in number but opposite to the corolla segments, is represented. The Ebenales, again, are the sympetalous representatives of what we have designated the "secondary branching tendency," with indefiniteness, typically, in all the the parts of the flower.

In a similar way we may observe the reflection in the Sympetalæ of the various stages in the evolutionary advance of the gynæcium, as we have traced it in the Archichlamydeæ—in the number of carpels, loculi, and ovules, and in the position of the ovary relatively to the rest of the flower.

The consequence of all this is, that there is a *primâ facie* presumption that the Sympetalæ are polyphyletic in origin,—unless, of course, it be supposed that they arose from pro-angiospermous ancestors quite independently of the Archichlamydeæ, a supposition which seems to be contrary to all scientific principle. We shall have occasion to return to this matter after we have dealt with the Sympetalæ in some detail; in the meantime, we make the reasonable assumption that the latter group are the direct descendants of Archichlamydeous ancestors.

In spite of the possibility that the Sympetalæ form a polyphyletic series, this series is synthetic in so far that its component members may be connected on the lines of certain well-marked progressive tendencies to biological advance.

These tendencies we proceed to trace, in relation to the classification of the group. They do not differ, fundamentally, in any way from the tendencies which we have observed at work in the Archichlamydeæ; but they differ in degree, as is to be expected, in view of the relatively high biological organization of the group. The tendency to oligomery has reached an advanced stage of realization, so that it plays but a secondary rôle in the Sympetalæ; it is the second fundamental principle, that of progressive adaptation to insect-visits, which is prominent. This fact emerges as we study the classification of the Sympetalæ exhibited upon the following page; the relations between the two modern accepted systems, those of Bentham and Hooker, and of Engler, are approximately indicated. With this latter purpose in view, the natural orders of the last cohort, Campanulatæ, have been shewn at length.

The merits and objections attaching to these systems will be discussed in the sequel; in the meantime, with the classification before us in tabular form, we may, in anticipation, draw attention to the following broad considerations:—

NOTE.—*re* Table on next page. *The arrangement of the cohorts in* ENGLER'S *System is that reproduced in* WILLIS' "FLOWERING PLANTS AND FERNS," second *edition*, 1904. *Attention will be called subsequenlly to one or two minor changes which have since been made.*

1. The tendency to economy in production is expressed principally in:—

CLASSIFICATION OF THE SYMPETALOUS DICOTYLEDONS,

ENGLER			BENTHAM and HOOKER		Approx. No. of Species.	Typical Characters, Displaying						
						ECONOMY IN PRODUCTION.				ADAPTATION TO INSECT VISITORS.		
	Cohort			Cohort		Stamens	Carpels	Loculi in ovary	Ovules per loculus.	Aggregation of Flowers.	Zygomorphy.	Fusion, giving special mechanisms.
PENTACYCLIDÆ	Ericales		HETEROMERÆ	Ericales	1739	C + C ↓ or C + staminodes or C	C $(\underline{G})$ or $(\overline{G})$	C	∞	No marked tendency; but dense clusters frequent.	Occurs, e.g. in some Rhododendra, especially in close inflorescences.	
	Primulales			Primulales	1180	C + staminodes or C, opp. petals	C $(\underline{G})$ or $(\overline{G})$	1	∞ – 1	Dense clusters; capitula.	Very rare	
	Ebenales			Ebenales	873	C+C+	C $(\underline{G})$ or $(\overline{G})$	C	2-3-4	No marked tendency	Rare.	
TETRACYCLIDÆ	Contortae		BICARPELLATÆ	Gentianales	3796	C to 2	2 $(\underline{G})$	2 to 1	∞	No marked tendency; conspicuousness attained often by enlargement of flower.	Very rare.	Gynandry in Apocynaceae and the highly specialized Asclepiadaceae.
	Tubiflorae	A		Polemoniales (excl. Solanaceae)	2570	C	2 $(\underline{G})$	C to 1	∞ – 1	No distinct general tendency.	Rare.	
		B		Lamiales	3551	Less than C by abortion of posterior stamen	2 $(\underline{G})$	2–4	1		Prevalent.	
		C, D		Personales (with Solanaceae)	6782			2–1	∞			
		E (Myoporaceae)		[in Lamiales]	86		2 – ∞ $(\underline{G})$	2 – ∞	few to 1		Common.	
	Plantaginales			'Anomalous' order, after Lamiales	200	C	2 $(\underline{G})$	2	∞ – 1	Dense spikes and heads	Absent	
	Rubiales		INFERÆ	Rubiales	4731	C	2 – ∞ $(\underline{G})$	2 – ∞	∞ – 1	Individual flower often much enlarged. Cymose clusters, capitula	Not frequent.	
	Aggregatae			Asterales	365	Less than C	3 – 2 $(\overline{G})$	1 fertile	1	Capitula	Prevalent, with asymmetry	
		Calyceraceae Compositae			11023	C	2 $(\overline{G})$	1			In outer florets.	General tendency to approximation and syngenesis of anthers, producing 'Pollen Presentation' mechanism.
	Campanulatae	Campanulaceae Goodeniaceae Candolleaceae		Campanales	1295		2 – ∞ $(\overline{G})$	2 – ∞	∞	Various,— enlarged solitary flowers, dense clusters, and capitula.	Flower often regular	
		Cucurbitaceae		[in Passiflorales]	650	often less than C	3 – C $(\overline{G})$	3 – C	∞ – 1	Various	Flower usually regular	Stamens variously united

(*a*). The reduction of the stamens to a number less than that of the corolla segments, following upon zygomorphy or asymmetry, *e.g.*, Tubifloræ, Aggregatæ.

(*b*). The progressive reduction of the calyx, to a pappus, or to zero.

(*c*). The reduction of the carpels to two (Bicarpellatæ and Asterales), the loculi to one, and the ovules to one (Asterales).

The tendency to progressive adaptation to insect-visits is reflected in:—

(*a*). The general introduction to zygomorphy, in Tubifloræ on the one hand, and in Aggregatæ and Campanulatæ on the other. Our two "types" of zygomorphy are thus both represented.

(*b*). The "pollen-presentation" mechanism, a general feature of the Campanulatæ.

With these general considerations as an introduction, we shall proceed, in future chapters, to consider the sympetalous cohorts in detail, and endeavour at the same time to apply the principles of floral evolution which have been enunciated.

SOME EXPERIMENTS ON ABSORPTION BY THE AERIAL PARTS OF CERTAIN SALT-MARSH PLANTS.

By Ann C. Halket, B.Sc.

FROM time to time since 1904 accounts have appeared in this Journal of the work carried out under the direction of Prof. F. W. Oliver on the ecology of the salt-marsh at Erquy in Brittany. In the accounts of 1906[1] and 1907[2] mention was made of the work done by the "physiological section" in estimating the osmotic pressure of the cell-sap of the typical plants *Salicornia* spp. and *Suæda maritima*. Most of the work was done with *Salicornia*.

Several species of *Salicornia* occur on the salt-marsh at Erquy and the individuals of some of the species, e.g., *S. ramosissima*, vary greatly in colour and form. Determinations of the osmotic pressure of the cell-sap of the aerial parts of the various plants were made and the results obtained, although they varied very much among themselves, all agreed in being very high. Ganong[3] found that the root hairs of "*Salicornia herbacea*," growing at the Bay of Fundy, were not plasmolysed by a 90% solution of the sea-water there, and Graves[4] working on *Ruppia maritima* found that its root hairs were not plasmolysed by a much stronger solution made by concentrating sea-water till it contained 110% sea-water. The values found for the osmotic pressure of the cell-sap of the succulent tissue of *Salicornia* from Erquy correspond to these, a result with which the values found for the root hairs by Hill[5] agreed. The values found varied in different plants, and in different parts of the same plant between certain limits. These limits correspond to osmotic pressures equal to that of 1·1 and 1·5 gramme-molecular solutions, *i.e.*, to solutions containing 6·4% and 8·7% of sodium chloride. These values are much higher than those found by Dr. and Mrs. Drabble,[1] for the salt-marsh plants *Aster*, *Plantago* and *Festuca*, from Burton Point, Cheshire.

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[1] F. W. Oliver. "The Bouche d' Erquy in 1906." New Phyt., Vol. V, p. 189, 1906.

[2] F. W. Oliver. "The Bouche d' Erquy in 1907." New Phyt., Vol. VI, p. 244, 1907.

[3] Ganong. "The Vegetation of the Bay of Fundy Salt and Dyke Marshes." Bot. Gaz., XXXVI, p. 358, 1903.

[4] Graves. "The Morphology of *Ruppia maritima*." Trans. Connecticut Acad. Arts and Sci., Vol. XIV, 1908.

[5] T. G. Hill. "Observations on the osmotic properties of the root hairs of certain salt-marsh plants." New Phyt., Vol. VII, 1908.

This high osmotic pressure is doubtless due to the fact that the sodium chloride absorbed by the roots accumulates in the cells of the succulent tissue. The analyses carried out by the members of the "chemical section," on the occasions referred to, show that the amount of sodium chloride present in the tissues was approximately sufficient to account for the high osmotic pressures found.

The variations found in the osmotic pressures of the different plants is then not surprising, if it is largely due to the purely passive accumulation of salt in the tissues, for one would expect the amount to vary with the age and vigour of the plant. This assumption is rendered more probable by the fact that the few estimations made of the osmotic pressure of the cell-sap in cotyledons of *Salicornia* and *Suæda* gave lower results, ·83 gm. mol. solution for *Salicornia*, and ·75 gm.-mol. solution for *Suæda*, than any made on mature plants.

The point clearly brought out by the osmotic pressure determinations, that I wish to lay stress on here, was that the osmotic pressure of the cell-sap of *Salicornia* was always considerably higher than that of sea-water. The same thing is also true of the osmotic pressure of the leaves of *Suæda maritima* and *Obione* (*Atriplex*) *portulacoides*.

The Bouche d' Erquy is covered by the sea about twelve times every fortnight during the spring tides; the number of hours the plants are covered each time varying with the height of the tide, but being, of course, greatest in the lower lying parts of the marsh and those nearer the sea, where the Salicorniæ grow most luxuriantly. The occurrence of the high osmotic pressure led one to ask whether it could not enable the plants to obtain water by absorption,[2] through the cells of the epidermis of its aerial parts, from the tides and from atmospheric moisture. It has long been known that many plants can absorb water through their leaves. This is well shown by the fact that flaccid leaves immersed in water, with the cut surface projecting, regain their turgidity. If then plants having an osmotic pressure of cell-sap corresponding approximately to that of a ·12 gm.-mol. salt solution are able to absorb water by osmosis, it seems probable that salt-marsh plants with their high osmotic pressures should be able to obtain water, not only from atmospheric moisture,[1] but also from the sea.

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[1] Drabble and Drabble. "The relation between the osmotic strength of cell-sap in plants and their physical environment." Bio. Chem. Journal, Vol. II, p. 117, 1907.

[2] After commencing these experiments, I saw the suggestion made by Drabble and Drabble in the paper referred to, that high osmotic pressures may enable plants to absorb water from the atmosphere.

In order to ascertain whether this is the case or not, experiments have been carried on at intervals during the summers of the last few years. Some few experiments were made at the Bouche d' Erquy itself, but the majority were carried out in the Botanical Laboratory of University College, London, on plants brought from Erquy and other localities. The plants were always brought to London in sods with a considerable amount of soil, so that they should continue as much as possible under natural conditions. In all the experiments, small plants, for the most part unbranched, were chosen, and great care was taken to use only those with the epidermis uninjured.

Absorption of water by the assimilating surface of a plant can be proved to have taken place if an actual increase in the weight of the plant is found after immersion; if there is an increase in the percentage of water in the tissues after immersion, or if, in the case of absorption from a salt solution, there is an increase in the strength of the solution after plants have been immersed in it.

In dealing with the question of absorption in *Salicornia*, most of the work was done with a view to finding out if there was an increase in the weight of individual plants after immersion. Some experiments were also made to find out the effect of immersion on the water-content of the plants, and an attempt was made to ascertain the effect of immersion of plants on the strength of a sodium chloride solution.

METHODS OF ESTIMATING THE ABSORPTION OF WATER BY AERIAL PARTS OF PLANTS.

(i.) *By Estimating the Differences in the Water-Content of Immersed and Unimmersed Plants.*

Plants, as nearly as possible alike, were chosen from the same place, the succulent parts of some were weighed, immediately dried at 100°C and weighed again. The succulent parts of others were immersed for a certain time in distilled water or in a 3% sodium chloride solution before they were weighed and dried. The percentages of water in the succulent parts of the plants were calculated from these weights. The percentage of water present in the succulent parts of those that had been immersed was greater than in those not immersed. This tends to show that water had been absorbed during immersion, especially as several plants were treated together to minimise the error introduced by the fact that plants from the same habitat do not necessarily contain the same percentage of water. The figures are given in Table I below:—

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[1] By atmospheric moisture is meant vapour from a very damp atmosphere as well as precipitated moisture, such as rain, dew and mist.

TABLE I.

Plant, Locality and Date.	Condition of Plant.	Weight in grammes of succulent part of plant.	Dry weight in grammes of succulent part of plant.	Percentage of water in succulent part of plant.
Suæda maritima at Erquy, 15/9/'09.	Leaves, freshly gathered	1·2300	0·1406	88·6%
	Leaves, after immersion of plant in distilled water	1·2585	0·1206	90·4%
Salicornia, from Erquy, 27/9/'09.	Plants fresh from the sod	3·0210	0·2950	90·2%
	Plants after immersion in distilled water ...	2·1770	0·1750	92·0%
	Plants after immersion in a 3% NaCl solution	1·1745	0·0990	91·6%

It will be seen from this table that plants that had been immersed contained, in their succulent parts, more than 1% more water than those fresh from the soil. The time of immersion was longer in the case of leaves of *Suæda* and the increase in water-content was greater. Plants of *Salicornia* immersed in distilled water had a slightly higher water-content than those in the salt solution, though the time of immersion was the same. This indicates that water was absorbed more slowly from the salt solution.

(ii.) *By Estimating the Difference in the Concentration of a Solution of Sodium Chloride before and after the Immersion of Plants.*

A number of plants of *Salicornia* were immersed in a 3% solution of sodium chloride. The plants were suspended in a well-corked flask containing the solution so that no evaproation should take place. They were left in the solution some time and then were removed and replaced by fresh plants. The strength of the solution was found at the beginning of the experiment, after the removal of the first set of plants and after the removal of the second. The solutions were diluted and titrated with a decinormal solution of silver nitrate. The following were the concentrations found:—

	Strength of NaCl solution.
At beginning of experiment	3·03%
After immersion of first lot of plants	3·12%
,, ,, ,, second ,, ...	3·24%

It will be seen from the above figures that the solution had increased in strength after the immersion of the first group of plants and had increased still further after the immersion of the second. The above figures are the result of a single experiment, and, since they as yet lack corroboration, too much stress should not be laid upon the actual increase of concentration. They suffice, however, to show that a certain amount of water had been removed from the solution by the plants, as care was taken that none should be lost by evaporation.

(iii.) *By Estimating the Difference in Weight in Individual Plants after Immersion.*

Plants were immersed in distilled water or in a 3% solution of sodium chloride and were weighed before and after immersion. The increase in weight found was always regarded as due to water absorbed, though there was the possibility that it might, in the case of immersion in salt solution, be in part due to sodium chloride diosmosing into the cells. This possibility was rejected because of the increase in concentration found in the experiment described above.

Method. In all experiments, except the preliminary ones, the plants were removed from the soil and their roots, with the small amount of soil adhering to them, were wrapped up in several layers of tin-foil. The succulent parts of the plants were then put into water or salt solution, taken out at once and dried as thoroughly as possible with filter paper. They were then weighed and this weight was taken as the first weight of the plant, so that if there should be any error due to imperfect drying it should be as much as possible nullified. The plants were then immersed in the liquids for varying periods of time, then dried as before and reweighed. During immersion the plants were suspended upside down in the liquids, care being taken that the level of the liquid should reach only half way up the lowest succulent internode. This precaution was taken so that increase of weight should be due only to absorption by living cells of the succulent parts of the plant. At the conclusion of any experiment the succulent part of the plant was cut off and the non-succulent part, etc. weighed. In this way the weights of the succulent part, before and after immersion, were obtained. In the later experiments the succulent parts were dried at 100°C and their dry weights found.

Preliminary experiments. In the preliminary experiments small plants were fixed, in the usual way, by corks into small bottles with a certain amount of soil. They were immersed in the liquids for a short time each day on three successive days; the rest of the day they were kept under a large bell-jar in the laboratory. The figures are given in the following Table:—

TABLE II.

Details of Plant.	Increase of weight in grammes after 3½ hours immersion	Decrease of weight in grammes in air in 19¾ hours.	Increase of weight in grammes after 4½ hours immersion	Decrease of weight in grammes in air in 20¼ hours.	Increase of weight in grammes after approximately 4 hours immersion.
Salicornia, from Erquy, Sept., 1907, immersed in 3% NaCl.	0·030	0·086	0·057	0·096	0·043
	Increase after 2 hours immersion	Decrease after 22 hours in air.	Increase after 1¾ hours immersion	Decrease after 20¼ hours in air.	Increase after 3 hours immersion.
Salicornia, from Tilbury, Nov., 1907, immersed in tap water (1)	0·045	0·132	0·050	0·188	0·095
(2)	0·029	0·199	0·038	0·195	0·100
(3)	0·030	0·306	0·026	—	—

It will be seen from these figures that each day the plants gained in weight during their period of immersion, though the gain in weight was less than the loss of weight during the rest of the day. Transpiration was not restricted by absence of root absorption, for the plants had been placed in the bottles with the soil attached to their roots undisturbed. In all the other experiments this was not the case, for, as stated above, the roots were removed from the soil and wrapped round with tin-foil, so that no root absorption could take place. These experiments are best divided into two groups, the first containing those that were immersed for a long period (17 to 24 hours), the second those that were immersed for a shorter period of a few hours. The experiments in which immersion extended over a long time were made to find out the capacity of the plant for absorption; those in which immersion was for a short period to see what was the amount of absorption that could take place in such a time as the plants might be wet with rain, etc. or covered by the lower tides.

For comparison of the results it was necessary to fix on some factor that was comparable for all plants. The percentage of water present in the succulent parts of the plants was found to vary so that the weight of the succulent part and its dry weight were both rejected as units of comparison, and the weight of the water present in the succulent part at the time of immersion was selected. Whenever possible, therefore, the difference in weight found has been calculated as a percentage of the water present at the time of immersion. In those cases where the dry weight was not found, the difference was calculated as a percentage of the weight of the succulent part of the plant.

I. EFFECT OF IMMERSION OF PLANTS IN LIQUIDS FOR A LONG PERIOD.

The plants were immersed and left overnight in distilled water or in a 3% solution of sodium chloride. They were weighed at the end of the period and a considerable increase in weight was found. The amount of the increase varied in different plants and there seems to be no relationship between the amount absorbed and the weight of the water or the percentage of water in the plant. In some cases the dry weight of the plant was not found, so that the increase in weight has been calculated as a percentage of the weight of the succulent part of the plant at the beginning of the experiment. Table III. gives the figures obtained.

TABLE III.

(*a*.) Plants immersed in distilled water.

Plant, locality from which it was obtained and date of experiment.	Approximate time of immersion in hours.	Weight of succulent part of plant in grammes at time of immersion	Dry weight of succulent part of plant in grammes.	Increase in weight in grammes after immersion	Increase calculated as a percentage of (1) weight of succulent part of plant (2) weight of water in succulent part.	
S. ramosissima,						
Erquy, 14/9/'09 (1)	17	0·5540	—	0·0789	14·24%	—
,, ,, (2)	17	0·8150	—	0·0618	7·58%	—
,, ,, (3)	17	0·4228	—	0·1128	26·68%	—
,, 25/9/'09 (4)	17	0·5108	—	0·0576	11·27%	—
,, 27/9/'09 (5)	20	0·1760	—	0·0290	16·47%	—
,, ,, (6)	20	0·1750	—	0·0530	30·29%	—
,, ,, (7)	20	0·2715	—	0·0485	17·86%	—
Salicornia, sp.,						
Blakeney, 20/7/'10 (1)	20	1·0724	0·0649	0·0730	6·80%	7·24%
,, ,, (2)	20	1·0254	0·0671	0·1168	11·39%	12·19%
,, ,, (3)	20	0·9120	0·0494	0·1306	14·32%	15·14%
,, ,, (4)	20	0·6334	0·0440	0·1140	18·00%	19·34%
,, ,, (5)	20	0·5376	0·0286	0·1064	19·79%	20·90%
,, ,, (6)	20	0·5536	0·0382	0·1844	33·31%	35·78%

(*b*.) Plants immersed in 3% NaCl.

Plant, locality from which it was obtained and date of experiment.	Approximate time of immersion in hours.	Weight of succulent part of plant in grammes at time of immersion	Dry Weight of succulent part of plant in grammes.	Increase in weight in grammes after immersion	Increase calculated as a percentage of (1) weight of succulent part of plant (2) weight of water in succulent part.	
S. ramosissima,						
At Erquy, 14/9/'09 (1)	17	0·6954	—	0·0890	12·8%	—
,, ,, ,, (2)	17	0·6852	—	0·0346	5·05%	—
,, ,, ,, (3)	17	0·4924	—	0·0414	8·4%	—
,, ,, 15/9/'09 (4)	17	0.5540	—	0·0789	14·2%	—
,, ,, ,, (5)	17	0·8150	—	0·0618	7.6%	—
,, ,, ,, (6)	17	0·4228	—	0·1128	26·7%	—
From ,, 27/9/'09 (7)	17	0·2073	—	0·0370	17·84%	—
,, ,, ,, (8)	17	0·2540	—	0·0470	18·50%	—
,, ,, ,, (9)	17	0·1325	—	0·0270	20·4%	—
Salicornia, sp.,						
From Blakeney, 20/7/'10 (1)	20	1·5792	0·1054	0·0072	0·45%	0·49%
,, ,, ,, (2)	20	0·5868	0·0421	0·0618	10·5%	11·3%
,, ,, ,, (3)	20	0·5071	0·0404	0·0383	7·5%	8·2%
,, ,, ,, (4)	20	0·5066	0·0365	0·0554	10·9%	11·8%
,, ,, ,, (5)	20	0·5552	0·0369	–0·0006	—	—
,, ,, ,, (6)	20	0·3970	0·0278	0·0074	1·86%	2·0%

It will be seen by examining the figures that plants immersed in distilled water absorbed, as a rule, a greater percentage of water than those in the salt solution.

The amount of water absorbed was greatly increased if the plants were left in air and allowed to transpire before immersion. Some plants were taken from the soil, prepared and weighed, and then left for 45 hours in air before they were immersed overnight in a 3% solution of sodium chloride. Plants so left differ little in appearance from fresh plants, only they are slightly limp. The "rigid skeleton" prevents any visible signs of flagging. The results obtained are given in Table IV.

TABLE IV.

Salicornia immersed in 3% NaCl.

Locality from which plants were obtained and date of experiment.	Weight in grains of succulent part of plant at beginning of experiment.	Dry weight in grammes of succulent part of plant.	Loss of weight in grammes in air in 45 hours.	Gain of weight in grammes in 3% NaCl. in approximately 24 hours.	Gain of weight calculated as a percentage of water in succulent part of plant at time of immersion.
Blakeney, 19/7/'10 (1)	1·0056	0·0694	0·2084	0·1516	20·8%
,, ,, (2)	0·7318	0·0562	0·1548	0·1180	22·7%
,, ,, (3)	0·6642	0·0477	0·2036	0·1802	43·6%
,, ,, (4)	0·7162	0·0528	0·1842	0·1850	38·6%
,, ,, (5)	0·4668	0·0328	0·1230	0·1426	45·8%
,, ,, (6)	0·3430	0·0266	0·1252	0·1026	53·7%

The increase in weight during immersion was approximately the same as the decrease due to transpiration, so that the average percentage of water in the plant at the end of the experiment was only a little lower than at the beginning. The time of immersion was much less than the time of transpiration. The calculated percentages of water in the succulent parts of the plants at the beginning of the experiment, after transpiration, and after immersion in the salt solution are given in Table V.

TABLE V.

Salicornia, sp.

Locality from which plant was obtained and date of experiment.	Percentage of water in succulent part of plant at beginning of experiment.	Percentage of water in succulent part of plant after transpiration.	Percentage of water in succulent part of plant after immersion.
From Blakeney, 19/7/'10 (1)	93·1	91·3	92·7
,, ,, ,, (2)	92·3	90·3	91·9
,, ,, ,, (3)	92·8	89·6	92·6
,, ,, ,, (4)	92·6	90·1	92·6
,, ,, ,, (5)	93·0	90·5	93·3
,, ,, ,, (6)	92·2	88·3	91·7

The difference in the amount of water absorbed, due to the difference in the turgidity of the cells, is seen by comparing the figures in the last columns of Tables III and IV.

Plants from Blakeney (Table III) left overnight in 3% sodium chloride solution, absorbed, on the average, 6·8%, while similar plants (Table IV) left in the air till tissues were somewhat limp, absorbed, on the average, 36·5% of the water present in the succulent part of the plant at the time of immersion. This increase in the amount of absorption would appear to be greatest during the first hours of immersion. This follows from an experiment in which plants were prepared and left to transpire all night before immersion in the salt solution. After 5½ or 6½ hours' immersion they were weighed, then re-immersed and weighed again next morning. The values obtained are given in Table VI.

TABLE VI.

Plant, locality from which it was obtained and date of experiment.	Weight in grammes of succulent part of plant at beginning of experiment.	Dry weight in grammes of succulent part of plant.	Loss of weight in grammes in dry air in approximately 22½ hours.	Gain of weight in grammes after immersion in 3% NaCl.		Gain of weight, calculated as percentage of water in succulent part of plant at time of immersion.	
				a 5½ hours. *b* 6½ hours.	15¾ hours.	1st period.	2nd period.
S. ramosissima.							
Blakeney, 3/10/'10 (1)	0·7990	0·0820	0·1216	*a* 0·1232	0·0568	20·69%	7·90%
,, ,, (2)	1·1794	0·1108	0·1190	*a* 0·0510	0·0278	5·37%	2·78%
,, ,, (3)	0·6287	0·0798	0·0718	*a* 0·0378	0·0188	7·92%	3·65%
S. europea, Linn.							
Blakeney, 3/10/'10 (1)	0·9890	0·0872	0·0826	*b* 0·0270	0·0180	3·30%	2·13%
,, ,, (2)	0·7596	0·0630	0·0662	*b* 0·0140	0·0030	2·22%	0·46%
,, ,, (3)	0·3270	0·0270	0·0238	*b* 0·0060	-0·0056	2·17%	—

In every case the amount of water absorbed during the first period, 5½ or 6½ hours, was greater than that absorbed during the second longer period, 15¾-hours. The amounts gained, calculated as percentages of the water present, in the succulent part of the plant at the time of immersion, are given in the last two columns. These plants did not, with one exception, gain as much in weight during the time of absorption as they lost in the period of transpiration.

II. Effect of Immersion of Plants in Liquids for a Short Period.

These experiments are best sub-divided into two groups; one in which plants were immersed for short periods of from 1½—3 hours, the other in which the plants were immersed for a longer period—but this period was interrupted every hour or so for the short time necessary to dry and weigh the plant.

(A). *Length of period of immersion,* 1½—3 hours.

The figures obtained from plants immersed in distilled water or a 3% solution of sodium chloride for periods varying in length from 1½—3 hours are given in Table VII. Some plants were used on two consecutive days, being left in the intervening time in the laboratory. Such plants are marked with an asterisk to indicate the second day they were used. When immersed in water the second day, these plants do not absorb more water than they did the first day, though their tissues are not so turgid. The reason for this may be that the difference between the osmotic pressure of the cell-sap on the two days scarcely affects the ratio existing between the osmotic pressure of the cell-sap and that of distilled water, and so does not affect the rate of passage of water intothe cells. Of the two plants immersed in salt-solution on two consecutive days, one absorbed the same amount, calculated per gramme of water in succulent per hour ; and the other about three times as much on the second day as on the first. The plants immersed for two consecutive periods on the same day, show the same result, as seen in Table VI, that is that the amount absorbed during the first period of immersion is greater that at the second.

TABLE VII.

(*a*.) Plants immersed in distilled water.

Plant, locality from which it was obtained and date of experiment.	Weight in grammes of succulent part of plant.	Dry weight in grammes of succulent part of plant.	1st period of immersion.		2nd period of immersion.		Increase calculated as percentage of water in succulent part of plant at time of immersion.	
			Increase in weight in grammes.	Time: Hours, Mins.	Increase in weight in grammes.	Time: Hours, Mins.	1st period.	2nd period.
Salicornia sp.								
From Erquy, 30/9/'09 (1)	0·1780	0·0125	0·0085	2.5	0·0025	1.30	5·1%	1·4%
,, ,, 1/10/'09 (1*)	0·1695	0·0125	0·0085	2.30	0·0050	2.15	5·4%	3·0%
,, ,, 30/9/'09 (2)	0·1605	0·0108	0·0080	2.0	0·0045	1.20	5·3%	2·8%
,, ,, 1/10/'09 (2*)	0·1440	0·0108	0·0065	2.35	0·0055	2.0	4·9%	3·9%

(*b*.) Plants immersed in 3% NaCl.

Plant, locality from which it was obtained and date of experiment.	Weight in grammes of succulent part of plant.	Dry weight in grammes of succulent part of plant.	1st period of immersion.		2nd period of immersion.		Increase calculated as percentage of water in succulent of plant at time of immersion.	
			Increase in weight in grammes.	Time: Hours, Mins.	Increase in weight in grammes.	Time: Hours, Mins.	1st period.	2nd period.
Salicornia, sp.								
From Erquy, 30/9/'09 (1)	0·2840	0·0296	0·0098	2.0	0·0022	1.35	3·8%	0·8%
,, ,, 1/10/'09 (1*)	0·2630	0·0296	0·0107	2.25	0·0073	2.22	4·6%	3·0%
,, ,, 30/9/'09 (2)	0·0950	0·0110	0·0030	2.0	0·0025	1.30	3·6%	2·9%
,, ,, 1/10/'09 (2*)	0·0890	0·0110	0·0100	2.30	0·0015	2.10	12·8%	1·7%
S. ramosissima.								
From Blakeney, 5/10/'10 (1)	0·6540	0·0668	0·0164	2.10	—	—	2·8%	—
,, ,, ,, (2)	0·6238	0·0565	0·0268	2.50	—	—	4·7%	—
,, ,, ,, (3)	0·4440	0·0432	0·0130	2.50	—	—	3·2%	—
S. europea, Linn.								
From Blakeney, 5/10/'10 (1)	0·3636	0·0322	0·0126	2.50	—	—	3·8%	—
,, ,, ,, (2)	0·3542	0·0310	0·0166	2.33	—	—	5·1%	—
,, ,, ,, (3)	0·3940	0·0266	0·0104	2.35	—	—	2·8%	—

(B). *Time of immersion divided into hourly periods.*

It was hoped in these experiments to find out what was the relationship that existed between the amount of water absorbed and the time of immersion. The plants were therefore suspended in the liquids, taken out, dried and weighed every hour. In some cases a longer interval elapsed, but in every case the exact time of immersion was taken. After weighing, the plants were replaced in liquids as soon as possible. From the experiments given above, Tables VI and VII, in which the amount absorbed in the first few hours was greater than in subsequent hours, it was thought possible that the amount of water absorbed diminished with the time of immersion. The results obtained did not bear out this assumption. In the plants experimented with, the amount absorbed each hour was small and varied from hour to hour; though, in some cases, it was nearly equal for consecutive hours. As these plants had been kept in the laboratory for about ten days, the fact that the amount of water absorbed was small may have been due to their decreased vitality, though the plants looked as healthy as ever. Certain other plants (2) immersed in 3% sodium chloride solution decreased in weight, but these were not sufficient to vitiate in any way the other results. The figures obtained are given in Table VIII.

TABLE VIII.— Plants immersed in distilled water.

Locality from which plants were obtained and date of experiment.	Weight in grammes of succulent part of plant.	Dry weight in grammes of succulent part of plant.	Time of immersion Hours, Minutes.	Increase in weight in grammes after immersion	Increase calculated as percentage of water in succulent part of plant at time of immersion.
Salicornia, Blakeney, 25/7/'10 (1)	0·3782	0·0237	1.0	0·0036	1·01%
			1.0	0·0028	
			1.0	0·0058	
			1.1	0·0058	
			1.0	0·0048	
			1.2	0·0058	
			16.6	0·0490	
,, ,, ,, (2)	0·3880	0·0236	1.2	0·0008	0·22%
			1.2	0·0008	
			1.0	0·0018	
			1.1	0·0008	
			1.0	0·0018	
			1.1	0·0028	
			16.16	0·0340	
,, ,, ,, (3)	0·4542	0·0286	1.0	0·0076	1·8%
			1.0	0·0090	
			1.0	0·0088	
			1.3	0·0102	
			1.0	0.0120	
			1.0	0·0152	
			16.15	0·0074	
,, ,, ,, (4)	0·4422	0·0249	1.0	0·0036	·86%
			1.0	0·0046	
			1.0	0·0036	
			1.0	0·0112	
			1.2	0·0106	
			1.3	0·0120	
			16.20	0·0096	
,, ,, ,, (5)	0·3357	0·0227	1.0	0·0051	1·63%
			1.0	0·0017	
			1.0	0·0023	
			1.0	0·0029	
			1.2	0·0027	
			1.6	0·0046	
			16.25	0·0506	
,, ,, ,, (6)	0·3790	0·0196	1.0	0·0054	1·5%
			1.0	0·0072	
			1.0	0·0066	
			1.0	0·0072	
			1.0	0·0062	
			1.4	0·0098	
			16.29	0·0220	
,, ,, ,, (7)	0·3789	0·0177	1.0	0·0100	2·77%
			1.0	0·0090	
			1.0	0·0042	
			1.0	0·0134	
			1.0	0·0174	
			1.0	0·0096	
			16.24	0·0178	
,, ,, ,, (8)	0·2486	0·0098	1.0	0·0032	1·34%
			1.0	0·0037	
			1.0	0·0051	
			1.1	0·0033	
			1.1	0·0037	
			1.4	0·0028	
			16.29	0·0044	

TABLE VIII., *continued*—Plants immersed in 3% NaCl.

Locality from which plants were obtained and date of experiment.	Weight in grammes of succulent part of plant.	Dry weight in grammes of succulent part of plant.	Time of immersion Hours, Mins.	Increase in weight in grammes after immersion	Increase calculated as percentage of water in succulent part of plant at time of immersion.
Salicornia, Blakeney, 26/7/'10 (1)	0·2062	0·0166	1.0 1.3 1.6 1.45 18.30	0·0028 0·0011 0·0006 0·0008 0·0103	1·48%
" " " (2)	0·1978	0·0151	1.0 1.1 1.11 1.38 18.50	0·0047 –0·0005 0·0004 0·0006 0·0102	2·57%
" " " (3)	0·2342	0·0177	1.0 1.2 1.13 1.40 18.32	0·0014 0·0010 0·0013 0·0005 0·0266	1·65%
" " " (4)	0·1720	0·0146	1.0 1.0 1.12 1.48 23·50	0·0019 0·0005 0·0072 0·0006 0·0236	1·2%
" " " (5)	0·2395	0·0222	1.9 1.8 1.41 56 24.18	0·0038 0·0022 0·0046 0·0024 0·0474	1·75%
" " 27/7/10 (6)	0·3434	0·0254	1.1 2.1 1.2 2.0	0·0015 0·0010 –0·0004 0·0030	0·47%
" " " (7)	0·2580	0·0221	1.0 2.1 1.0 2.0	0·0012 0·0004 0·0000 0·0006	0·51%
" " " (8)	0·2613	0·0196	1.1 2.1 1.14 2.4	0·0010 0·0011 0·0012 0·0030	0·41%

In some cases, at the end of the hourly readings, the plants were left all night immersed in the liquid. The ratio between the amount of water absorbed during the long period and that absorbed during the sum of short periods varies, but in the majority of cases the amount absorbed when left immersed all night was greater than that absorbed in the short periods. This is contrary to the results given in Table VI, but the conditions differed in that the succulent tissues were turgid here and not turgid in that experiment.

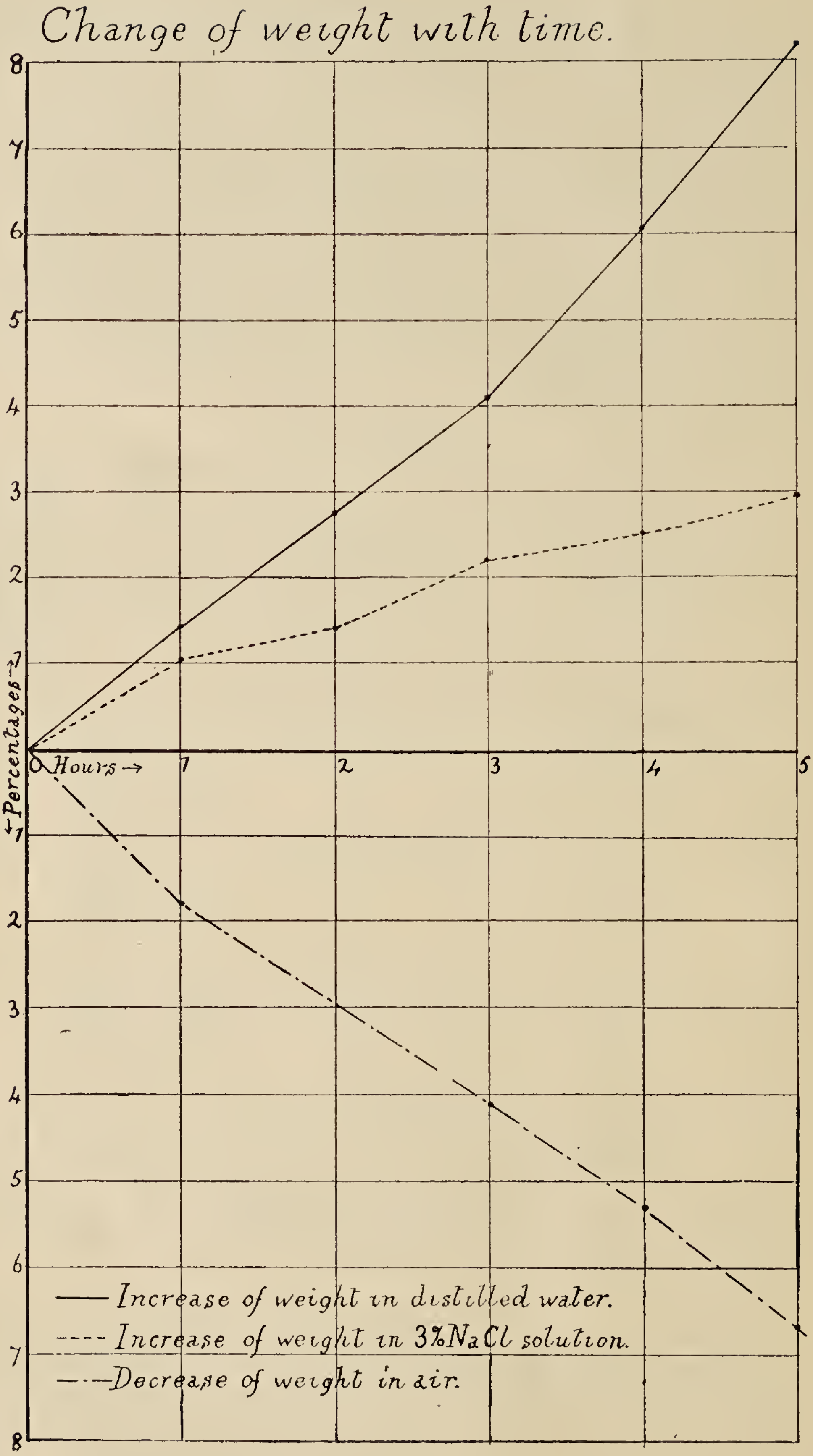
Control plants were left in air and weighed at short intervals. The decrease in weight due to transpiration was, on the whole, rather less than the average increase of weight after immersion in water for the same time, though at first the loss in weight was greater than the gain. The figures are given in Table IX, and the decrease has been calculated as a percentage of the water present in the succulent part of the plant at the beginning of the experiment.

TABLE IX.

Locality from which plants were obtained and date of experiment.	Weight of succulent part of plant.	Dry weight of succulent part of plant.	Time: Hours, Mins.	Decrease in weight of plant in air.	Decrease calculated as a percentage of water in succulent part of plant at beginning of experiment.
Salicornia, sp. Blakeney, 27/7/'10 (1)	0·3649	0·0274	1.0	0·0093	2·76%
			2.6	0·0114	
			1.22	0·0054	
			1.6	0·0064	
„ „ (2)	0·2200	0·0187	1.0	0·0032	1·59%
			2.0	0·0035	
			1.22	0·0015	
			1.6	0·0016	
„ „ (3)	0·1982	0·0151	1.0	0·0006	·33%
			2.0	0·0019	
			1.25	0·0017	
			1.5	0·0016	

An attempt has been made to represent graphically the relations between the amount of water absorbed and the time of immersion in water and in the salt solution; also between the amount of water lost in air through transpiration and the time occupied.

In these "curves" the values for the abscissæ were obtained by adding together the values obtained for the different plants given in Tables VIII and IX, and treating the totals as one result. The gain or loss of weight was then calculated as a percentage of the water present at the beginning of the experiment. These percentages are plotted against the time.


Change of weight with time.
8
7
6
5
4
3
2
1
0
Hours →
1
2
3
4
5
← Percentages →
1
2
3
4
5
6
7
8
Increase of weight in distilled water.
Increase of weight in 3% NaCl solution.
Decrease of weight in air.

EFFECT OF IMMERSION IN SALT SOLUTION ON SOME NON-HALOPHYTIC PLANTS.

Non-halophytic plants similarily treated and immersed in a 3% sodium chloride solution lost instead of gained in weight. This is no doubt due to the fact that water passes out from the cells of the plant into the solution, since the osmotic pressure of their cell-sap is less than that of the salt solution.

Some mesophytic seedlings, *Chenopodium* sp., were exposed to air till slightly flagged, and then immersed overnight, some in distilled water and others in a 3% sodium chloride solution. Those in water increased in weight while those in the salt solution decreased in weight.

Leaves of *Primula*, *Tradescantia* and *Myriophyllum* were also found to decrease in weight when immersed for 3—4 hours in a 3% sodium chloride solution.

On examination of the tables given it will be seen that there is a great variation in the results obtained from different plants in all the experiments. The reason of this variation is not known, for the plants experimented with were all treated alike, and as far as possible similar plants were used for any one experiment. So far as can be seen the amount of water absorbed does not depend on the amount of water in the plant,—or on the percentage of water present. It may be that the amount absorbed depends on the surface area of the plant, but unfortunately in these experiments no measurements of surface area were taken. Also, the variations in the amount of water absorbed may correspond to variations of osmotic pressure in the cell-sap, but no osmotic pressure estimations were made on these plants.

RESULTS.

In spite, however, of the variation of the figures given in the tables, from their consideration the following results may be deduced :—

1. Plants of *Salicornia* can absorb water through their epidermal cells from distilled water and from a 3% solution of sodium chloride. The amount absorbed varies with individual plants and is greater from distilled water than from the salt solution (Tables III, VII and VIII).

2. The amount of water absorbed is greatly increased if, before immersion, the plants are allowed to transpire without being able to obtain any water by root-absorption. Plants so treated usually absorb more water when they are first immersed than afterwards.

3. No quantitative relations can be deduced between the amount of water absorbed and the time of immersion, the weight of the succulent part of the plant, the weight of water in the succulent part of the plant or the dry weight of the plant.

Some quantitative results might possibly have been obtained if the surface area had been used for comparison, but no measurements of area were taken.

4. This absorption is due to the high osmotic pressure of the cell-sap since non-halophytic plants lose water during immersion.

Many gaps are left by these experiments, but they are, perhaps, worth recording as they show that certain typical salt-marsh plants, especially under conditions of drought, are capable of absorbing water through the epidermal cells of their aerial parts, not only from precipitated atmospheric moisture, but also from a salt solution approximating in strength to that of the sea. No experiments were made to see what absorption took place from sea-water itself.

It is impossible to tell without further experiment what is the importance of the part played by this method of absorption in the life of these plants. Their root-system is small in proportion to their size and it is probable that the amount of water absorbed by the roots is proportionally small. The water obtained from "atmospheric moisture" through absorption by its aerial parts may compensate the plant for this smallness of root-absorption. It is not suggested that the quantity of water absorbed from the sea by its aerial parts is of great importance to the plant under ordinary conditions, for this amount is small. It is suggested, however, that the water absorbed in this way may be especially useful to the plant in times of drought. Under these conditions the amount absorbed is greater, and the neceessity for it is increased as the amount of atmospheric moisture available is reduced. It is probable also that under conditions of drought root-absorption is diminished. For if, as is generally accepted, root-absorption is due to "osmosis," the rate at which water passes into the root-hairs must in part depend on the difference of concentrations of their cell-sap and the surrounding liquid. Hill[1] has shown that the osmotic pressure of the root-hairs of *Salicornia* seedlings can adjust itself in response to a change in that of the surrounding medium. There is no reason, however, to suppose that the *ratio* between the osmotic pressures of the cell-sap and that of the surrounding liquid remains the same.

[1] Op. cit.

That the amount absorbed in this way can in no way replace normal absorption is shown by the facts recorded in 1906, when it was pointed out that the plants, probably because of the very dry summer, had only grown to about half the height they had attained the year before.

The water absorbed by its aerial parts must pass into the plant by osmosis through the epidermal cells and these are so formed that their walls offer little resistance to its passage. Both in *Suæda* and *Salicornia* the walls of these cells are unthickened and are covered only by a thin cuticle comparable to that found in *Zostera*. The presence of large cellulose tracheal-like cells in some species of *Salicornia* has long been known. These cells run from the aqueous tissue surrounding the stele, through the palisade tissue and in some cases came into contact with the epidermal cells. They are isolated from each other and from the anastomosing vascular system of the succulent tissue. Various functions have been assigned to them. Ganong suggests that they are air-storing tracheids, Warming and others that they are for water-storage, but it is now suggested that it is possible that their function is to facilitate the passage of the water absorbed by the epidermis to the aqueous tissue. This, however, is only a suggestion, as further experiments must be made to elucidate their function.

I wish here to express my thanks to Miss E. N. Thomas and to Professor F. W. Oliver for their helpful criticism of this paper.

ON SOME POINTS OF RESEMBLANCE BETWEEN GNETALEAN AND BENNETTITEAN SEEDS.

By Emily M. Berridge, B.Sc.

[Text-Figs. 1—5].

In the spring of the year 1908 some ovules of *Gnetum gnemon*, originally obtained from Kew, furnished me with a series of sections which showed a curious blocking of the micropyle by secondary growth of the tissues of the wall after the time for fertilization was past.

This fact of the closing of the micropyle in the young seed is mainly of interest on account of the light it may throw on

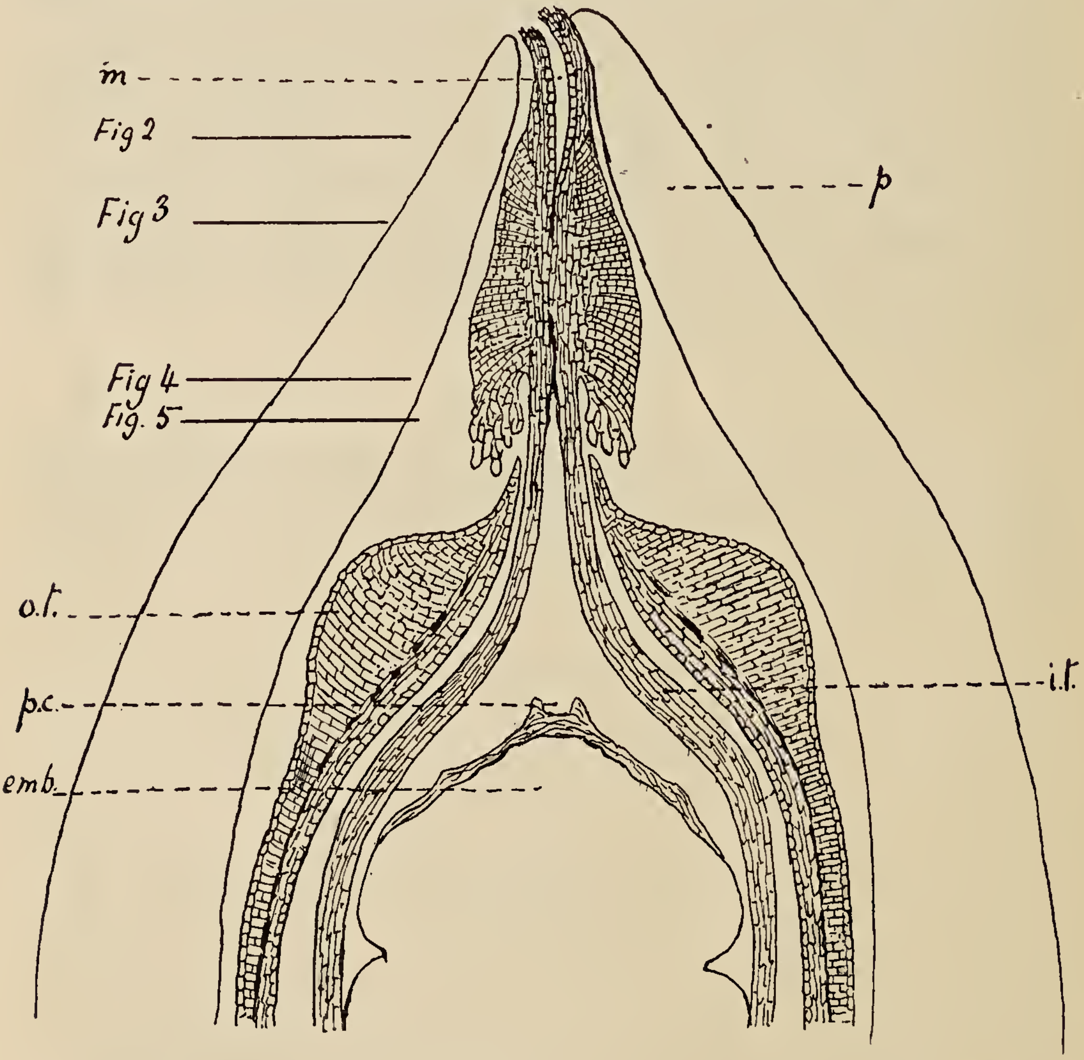


Fig. 1. Longitudinal section through upper half of young seed of *Gnetum gnemon*. *p*, perianth; *o.t.*, outer integument; *i.t.*, inner integument; *p.c.*, pollen-chamber; *emb.*, embryo; *m.*, micropyle. The levels of the transverse sections represented in Figs. 2, 3, 4 and 5 are indicated. ×25.

the condition of certain Bennettitean seeds in which, as Dr. Scott remarks in the "Studies in Fossil Botany," the micropyle is usually closed. Indeed the sections through the apex of these seeds of *Gnetum* show in many respects resemblances to the drawings of *Bennettites Morierei* published by Professor Lignier[1] in 1894.

The ovules of *Gnetum gnemon* in question were about 7 m.m. in length; the embryo-sac was nearly filled with a thin-walled tissue, but no trace of embryos could be detected.

Transverse sections through the extreme apex show a withered micropyle, the wall of which consists of three or four layers of flattened cells, bearing internally a well-marked columnar epidermis. This is surrounded by the edge of the perianth, which also shows signs of withering.

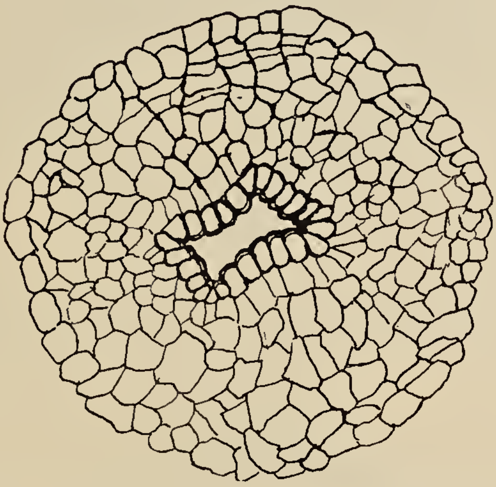


Fig. 2. Transverse section near the tip of the micropyle. × 150.

Fig. 2 represents the micropyle just below the withered portion. Here the wall is six or eight cells thick, the thickening being apparently partly due to tangential divisions of the cells below the outer epidermis. Lower down similar divisions take place in the cells beneath the internal epidermis with the result that the micropyle is reduced to a mere slit. Lower down still the outgrowth of some of these cells into the small cavity completes the blocking of the passage, as is clearly shown in Fig. 4, and in cross-section we appear to get a solid cylinder of tissue (Fig. 3).

Similar growth and proliferation of the cells takes place in the outer layers of micropylar wall. Here a kind of flange is produced, which fits over the upper edge of the outer integument. In the longitudinal section figured, contraction due to fixation in alcohol accounts

[1] Lignier, O. ('94). Structure et Affinités du Bennettites Morierei, Mem. Soc. Linn. Normandie, Vol. xviii., Ser. 2. 2.

for the distance between the tip of the outer integument and the flange. The latter extends downwards in a fringe of long hairs which, normally, completely close the crevice between the inner and outer integuments. Thus the delicate structures within the young seed are effectively guarded from the entrance of fungal spores or minute insects either through this interstice, or by way of the micropyle. The micropylar passage is only blocked for a short distance, but when it reappears the cells lining it are torn and crushed, and only at a lower level can a very delicate internal epidermis be distinguished (Fig. 5).

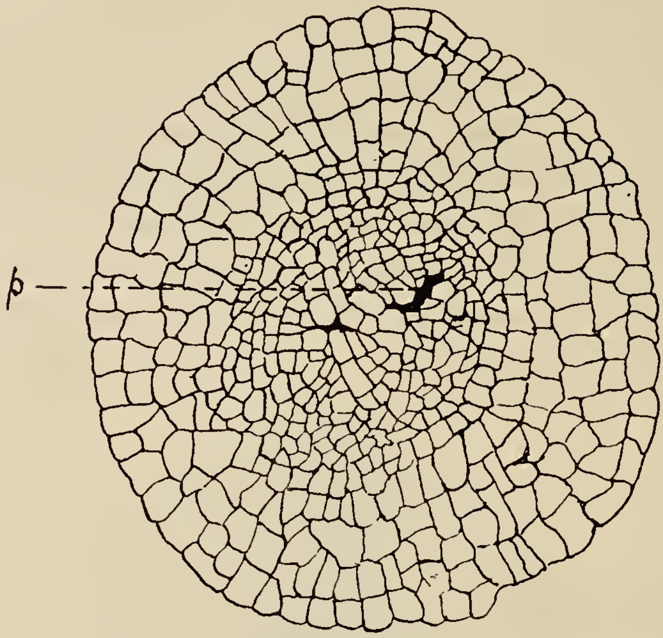


Fig. 3. Transverse section showing the micropyle completely blocked, the passage (*p*.) only indicated by the crushed remains of cells. × 125.

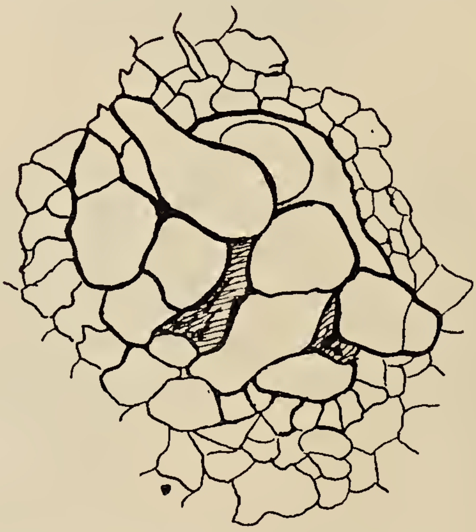


Fig. 4. Transverse section at point where micropylar canal begins to reappear, showing ingrowing cells on one side. × 330.

Sections passing through the apex of the nucellus show four concentric rings of tissue—the perianth, the outer and inner integuments, and the border of the small lysigenous pollen-chamber, which at this stage is not much more than a shallow depression among the withered cells of the nucellar apex.

Turning now to Professor Lignier's account of the seed of *Bennettites Morierei*, we find that it is described as possessing a micropyle free at the apex, but blocked lower down by a tissue which is regarded as the nucellar beak; below this, the passage reappears again, with walls which show signs of lysigenous degeneration on the inner surface. Dr. Wieland,[1] however, finds in the American types a micropyle which is open throughout. This difference suggests that the micropyle of *Bennettites* became blocked after fertilization just as in *Gnetum gnemon*; in that case the tissue known as the nucellar beak in Professor Lignier's seeds would correspond to the secondary closing tissue in *Gnetum*, and Dr. Wieland's figure might represent the seed of *Bennettites* at a younger stage.

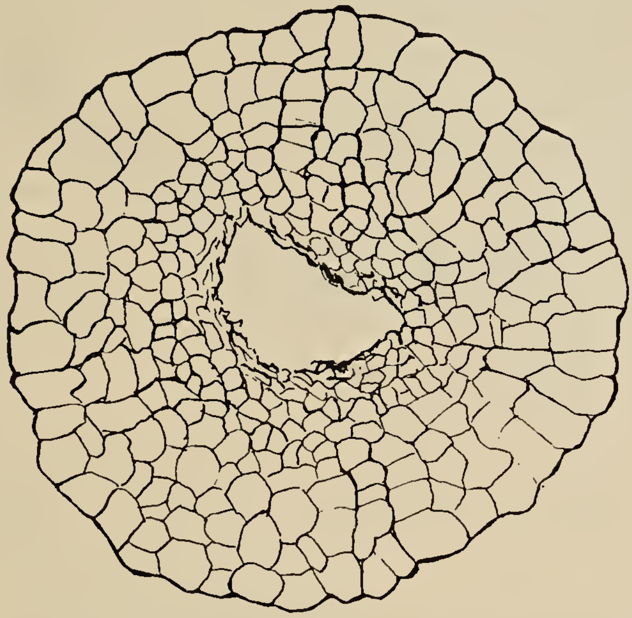


Fig. 5. Transverse section of micropyle at lower level showing no definite internal epidermis, but a cavity apparently lysigenous. ×150.

Professor Lignier himself draws attention in a note[2] to the likeness of the Bennettitean ovule to a Gnetalean type of seed, but rejects this interpretation in favour of a Cycadean one, because, in the first place, the micropylar tube is solid at one point, and secondly, because the lower part of the tube does not appear to be lined by a definite epidermis. But both these objections become points of resemblance between the Bennettitean and Gnetalean seeds if the above suggestion is correct. Moreover, the fact that Professor Lignier found no pollen-grains in the canal, nor in the "vast cavity" above the nucellus into which it opened, but found two black globules, which he suspected to be pollen-grains, in a small depression among the torn tissues just above the embryo, certainly points to the possession by the fossil seed of a small lysigenous pollen-chamber comparable with that of the Gnetales.

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[1] Wieland, G. R. American Fossil Cycads. Washington, 1906.

[2] loc. cit. p. 50.

Other resemblances too may be traced between the two seeds. Professor Lignier's "assise rayonnante," the continuity of which with the tissues of the upper part of the micropyle is admittedly doubtful, corresponds exactly in position with the radially expanded portion of the outer integument of *Gnetum* (Fig. 1, *o. t.*), whose upper edge is normally buried among the hairs of the flange above; also the apical part of the micropyle with its columnar epidermis and angular cavity is very similar in both.[1] The sudden change in *Gnetum* in the character of the micropylar wall below the flange to a delicate membrane, the lower part of which fuses so completely with the nucellus that the limit between the two cannot be traced in the ovule, also corresponds with the description of the layer lining the canal and so-called pollen-chamber of *Bennettites*, which is regarded as nucellar both by Professor Lignier and Dr. Wieland.

If this interpretation of the seed of *Bennettites*, originally suggested by Professor Lignier himself, is the correct one, we have to add to the important resemblances already generally recognized, such as the possession of a dicotyledonous embryo, and the occurrence of pro-anthrostrobili in both groups—the fact that they possess seeds which are practically identical in type.

---

[1] Mrs. Thoday drew attention to these points of resemblance in her paper on *Gnetum africanum* read at the British Association meeting at Sheffield last year.

Occasional Note.

We are asked to call attention to the advertisement of the Vincent Stuckey Lean Scholarship in Botany at the University of Bristol, appearing on the inside of the front cover.

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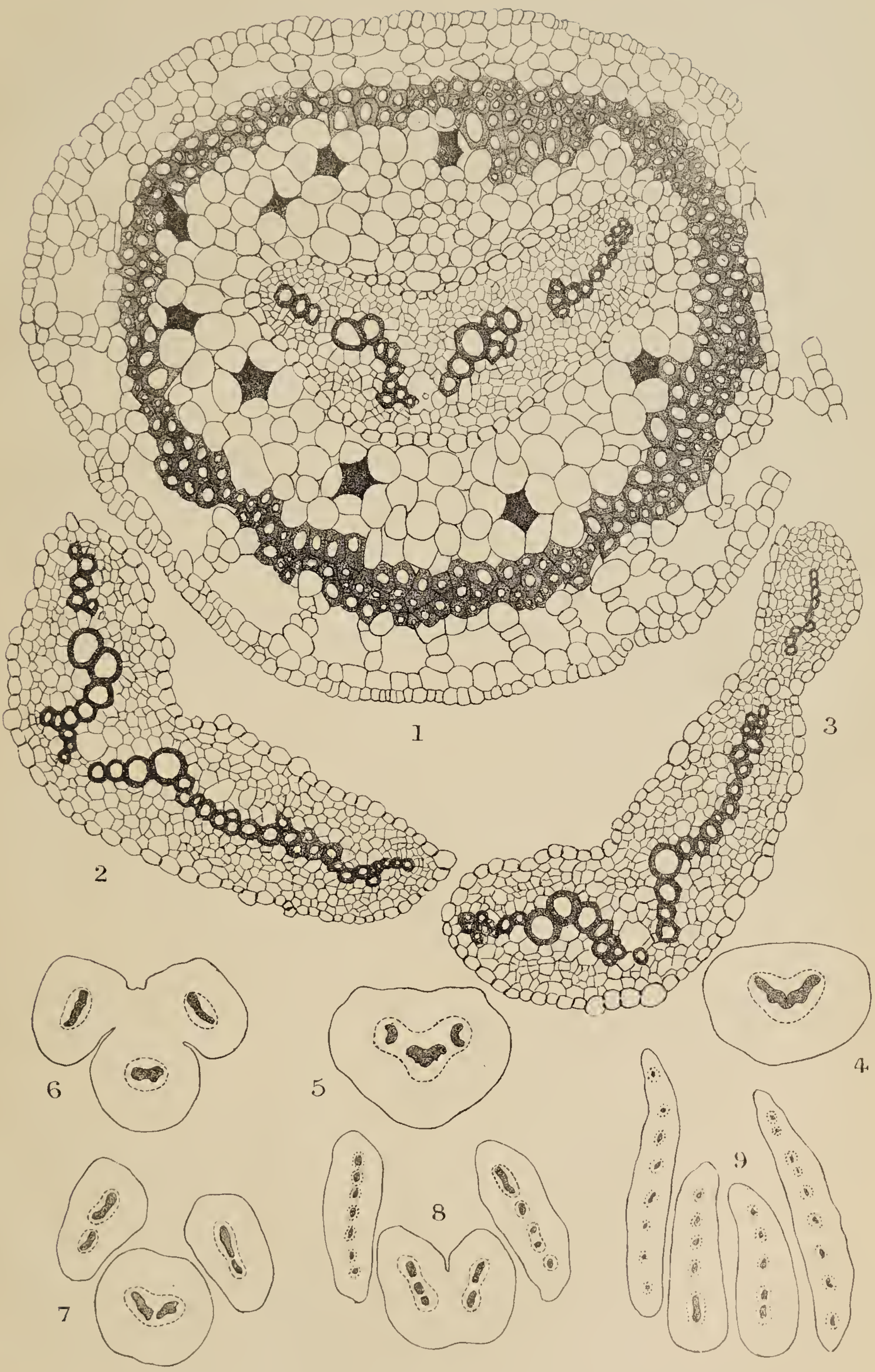

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FLORAL EVOLUTION; WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

BY H. F. WERNHAM.

III. THE PENTACYCLIDÆ.

THIS group of Engler's system corresponds with the Heteromeræ of Bentham and Hooker, and, like the latter, includes three cohorts—Ericales, Primulales, and Ebenales; these cohorts are identical in the two systems. For convenience of reference, the typical characters, especially in so far as the numbers of the various parts are concerned, have been summarized in the annexed table (see next page), and the relation between the two systems of classification has been shewn.

The Pentacyclidæ stand alone among the Sympetalæ in the character of the andrœcium. This consists typically of two whorls of stamens, the number of members in each whorl equalling the number of petals; and, in some cases, the presence of an ancestral third whorl may be indicated by the obdiplostemonous arrangement. In other cases the stamens are isomerous with the petals, but anteposed to them; not infrequently an outer alternating whorl of "staminodes" is present. In the Ebenales the andrœcium is frequently polycyclic and the stamens indefinite in number. Only rarely are the stamens equal in number to the petals and arranged alternately with them.

The gynæcium is usually either isomerous with the corolla, or polycarpellary; only very rarely, in any case, is the ovary bicarpellary.

The corolla, we shall see, retains the polypetalous arrangement in not a few instances; and for this reason, coupled with the diplostemony of the andrœcium, we shall be prepared to find in the

THE PENTACYCLIDÆ.

Cohort	ENGLER	BENTHAM and HOOKER	Approx. no. of species.	Corolla	Stamens	Pistil		
						Carpels	Loculi	Ovules per loculus
ERICALES	Lennoaceae	Lennoaceae	5	(5-8)	C	$(\underline{C})$	2C-∞	1
	Pyrolaceae: Saprophytes	Monotropeae	30	5-4 usually free sometimes united.	C+C ↓	$(\underline{C})$	C	∞
	Pyrolaceae: Green plants	Ericaceae						
	Clethraceae		25	5 free	C+C ↓	$(\underline{3})$	3	∞
	Ericaceae: Rhododendroideae Arbutoideae Ericoideae		1350	(5-4) sometimes free	C+C ↓	$(\underline{C})$	C	∞-1
	Ericaceae: Vaccinioideae	Vaccinieae				$(\overline{C})$		
	Epacridaceae	Epacrideae	320	(5) very rarely free	C alt. w. petals	$(\underline{C-2})$	2C-2	∞-1
	Diapensiaceae	Diapensiaceae	9	(5)	C alt. w. petals	$(\underline{3})$	3	∞-few
PRIMULALES	Myrsinaceae	Myrsineae	550	(4-6) rarely free	C opp. petals	$(\underline{?})$ or $(\overline{?})$	1	∞-few
	Primulaceae	Primulaceae	350	(4-9)	C opp. petals	$(\underline{?})$ rarely $(\overline{?})$	1	∞-2
	Plumbaginaceae	Plumbagineae	280	(5) sometimes free	C opp. petals	$(\underline{5})$	1	1
EBENALES	Sapotaceae	Sapotaceae	370	(n+n) n=2,3 or 4 or (5)	C opp. petals or C+C or ∞	$(\underline{2-\infty})$	2-∞	1
	Ebenaceae	Ebenaceae	280	(3-7)	C+C or C+C+... rarely C alt. w. petals	$(\underline{2-\infty})$	2-∞	1-2
	Symplocaceae	Styraceae	150	5-4 subpolypet.	∞	$(\overline{2-5})$	2-5	few
	Styracaceae		73	(5-4) often nearly free	7-12 uniseriate	$(\underline{2-5})$	2-5	1-few

Pentacylidæ a transitional group between Archichlamydeæ and Sympetalæ. We may now proceed to discuss each cohort in turn.

ERICALES.

From the aspect of the economy principle, these will readily be regarded as a primitive group relatively to the Sympetalæ. A glance at the table will reveal the fact that in the bulk of the species two whorls of stamens are present, the arrangement being typically obdiplostemonous. This arrangement is reflected in the Pyrolaceæ, Clethraceæ and Ericaceæ, which groups include nearly three-fourths of the total number of species in the cohort. Isomery of the andrœcium is typical of the relatively large order Epacridaceæ; the stamens equal the petals in number also in the small degenerate order Lennoaceæ; and in the Diapensiaceæ, what may be an intermediate stage[1] is represented, in which an isomerous whorl of stamens alternates with an outer whorl of staminodes placed opposite to the petals.

The gynæcium is multilocular, and usually multiovulate. In the bulk of the species the carpels are isomerous with the corolla; in Clethraceæ and Diapensiaceæ the transitional number 3 appears; but a bicarpellary ovary is a very rare occurrence in this cohort. Reduction in the number of ovules is traceable within the limits of the two largest orders, Ericaceæ and Epacridaceæ, and in Diapensiaceæ. The larger of the two tribes in which Bentham and Hooker divide their Epacrideæ is distinguished by the uniovulate condition of each loculus of the ovary; in Lennoaceæ this condition is the invariable rule.

From the foregoing statements it is clear that the tendency to economy in production of parts, so important a feature in the Archichlamydeæ, is still actively at work in the Ericales. The significance of this, particularly in regard to the linking of the Archichlamydeæ with the Sympetalæ, is emphasized by the retention of a polypetalous corolla in not a few species of this cohort; polypetaly characterizes the Clethraceæ, most Pyrolaceæ, some Ericaceæ, and a few Epacridaceæ. Correlated with this ancestral trait is the position of insertion of the stamens; these are hypogynous in most of the species concerned, and free of the corolla, or adherent to its base only. In the Epacridaceæ, however, the stamens are frequently epipetalous, either in the tube, or in some cases, at the throat of the corolla.

As is to be expected, a cohort so actively occupied, so to speak, with the tendency to economy does not display in any high degree the general adaptations to insect visits which were summarized in the last chapter. The corolla tube, we have just seen, is not yet established as a perfectly constant feature, although sympetaly characterizes the large majority of the species. Conspicuousness is attained, speaking generally, by the aggregation of relatively small flowers into more or less dense clusters, spikes, &c.; and this, in some rare cases—notably in the Rhododendra—has been followed by Zygomorphy.

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[1] But see *infra* p. 152, on the significance of staminodes.

The tribe Vaccinioideæ, the Vaccinieæ of Bentham and Hooker, is unique among the Ericales in the character of inferiority of the ovary; and on the lines we have laid down, this would appear to throw some measure of doubt upon the propriety of associating this extensive group so closely with the Ericales. We shall return to them shortly; we may remark in the meantime that their flowers differ in no essential way from those of the other Ericaceæ, save in the relative position of the ovary.

The Ericales, with their double staminal whorl, multilocular ovary, and frequent presence of a more or less conspicuous disc, seem to have undoubted affinities with the Geraniales. In both cohorts the same tendency to reduction in the number of stamens and carpels is observable; and in many ways the Geraniales are considerably more advanced than the Ericales. For the bicarpellary condition of the ovary is realized in an extensive section, *viz.*, Engler's group D, of the former cohort, which includes the large natural order Polygalaceæ. The latter, moreover, are remarkable for their zygomorphic flowers, and zygomorphy is by no means rare among the other orders of Geraniales. The tendency to cohesion of filaments, again, has already been referred to as a distinguishing feature of this cohort. Lastly, the presence of one or two ovules only in each loculus of the ovary, in the large majority of the Geraniales, represents a material advance in the direction of economy as compared with the Ericales, in which the number of ovules is usually indefinite.

The Ericales, on the other hand, are very distinct and specialized both in habit and in habitat; the natural orders and larger subordinate groups can be readily recognized, in most cases, by the habit alone. That of the tribe Ericoideæ is so characteristic as to have given rise to a general botanical term—the *ericoid* or *heath* habit. The shrubby and arboreal members of the other ericaceous tribes, with their typically entire, elliptic, leathery leaves tending to a rosette arrangement upon the twigs, are recognizable with little difficulty. The Epacridaceæ, again, are mostly small shrubs with narrow rigid leaves, representing in Australia and Tasmania the Ericaceæ of other regions. The low rhizomatous growth and small half shrubby, half herbaceous habit of the green-leaved Pyrolaceæ and the alpine and arctic Diapensiaceæ, with their flowers borne usually in scapes, are clearly distinctive features; while the non-green Pyrolaceæ (Montropeæ) and the

Lennoaceæ have reached a climax of specialization in the complete loss of chlorophyll and the adoption of a saprophytic mode of existence.

Above all it must be borne in mind that the Ericales have, in the bulk of their constituent species, taken the fundamental step in the direction of adaptation for insect visits—namely, fusion of the petals to form a sympetalous corolla. This step from the archichlamydeous ancestral stock was taken, we must presume, at a relatively early stage in the progress of the tendency to economy—before the latter had proceeded so far as to "produce" the Geraniales, if we may so express it (see Fig., p. 151). This found expression in the typical ericalian flower with two whorls of stamens, multilocular ovary, and numerous ovules. The continued working of the economy tendency within the cohort achieved its final result in the "production" of the epacridaceous flower, with a single whorl of stamens, and, in over 65% of the species of Epacridaceæ, with but a single ovule in each loculus of the ovary. Sympetaly has, further, been followed in the last-named natural order by epipetaly of the stamens, and this, as we have already seen, is significant in connection with economy of material (*supra*, p. 82). In Diapensiaceæ, too, the stamens are epipetalous. The floral character of the Epacridaceæ, together with their specialized habit and limited distribution, leads us to the supposition that this natural order represents the climax of evolutionary tendencies along the ericalian line; and, further, we are driven to the conclusion that the latter ends blindly at this point, in view of the fact that there seem to be no groups among the rest of the Sympetalæ which reveal any indication of having been derived from a sympetalous ericalian stock. Thus viewed, the Ericales represent one of the threads, and that the most primitive, in the polyphyletic origin of the Sympetalæ.

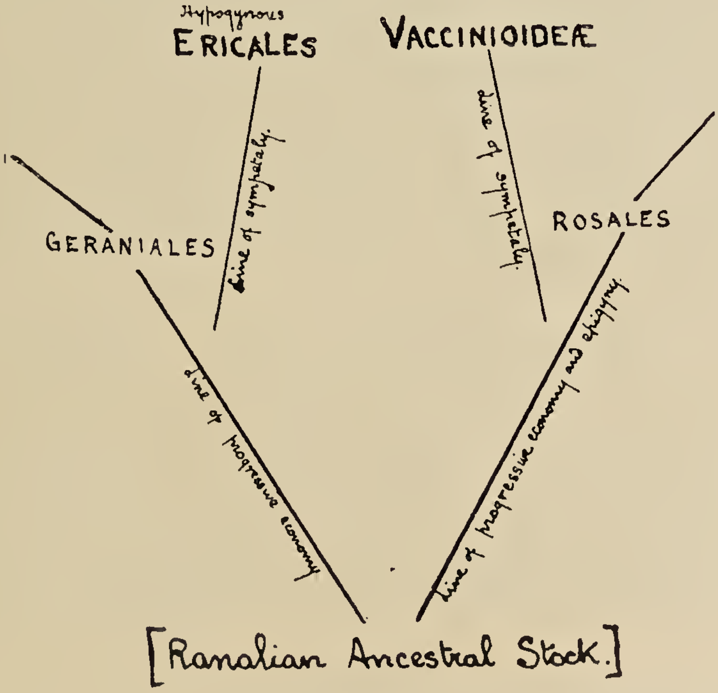
We have now to consider the origin and affinities of the Vaccinioideæ. This group has hitherto been associated closely with Ericaceæ, and is included by Bentham and Hooker as a natural order—Vaccinieæ—of the Ericales; Engler goes so far as to include them in the Ericaceæ, giving them tribal status only. This close association is based on the great similarity in structure between the flowers of the hypogynous Ericaceæ and Vaccinioideæ—a similarity which extends not only to the habit and number of stamens, carpels, and ovules, but even to the shape of the corolla and to the details of the structure of the stamens, with their poral dehiscence, appendages, &c. The position of the ovary relatively to the other floral organs has thus been ignored.

On the lines we have laid down in our opening chapters, however, it is urged that the occurrence of epigyny in so extensive a group may not be so lightly set aside. Epigyny, we have already suggested, is the reflection of a broad general principle—the Calycifloral tendency—correlated with the principles both of economy and of adaptation to insect visits. Now the Geraniales represent a line of evolutionary advance, delineated for the most part by the former principle, that of economy; there is no trace of epigyny in the Geraniales. In the search for the sign of an archichylamydeous ancestral stock for the Vaccinioideæ it would seem that we should attempt to find a line characterized by the tendency to economy, coupled with the tendency to epigyny; the working of the former would account for the similarity between the Vaccinioideæ and the rest of the Ericales in the numbers of the stamens and carpels. Such a line is indicated in the progress from Ranales to Rosales, and within the latter heteorgenous cohort itself. Most of the Rosales have two whorls of stamens, each isomerous with the corolla; in many, again, the carpels also are isomerous, although in this regard the archichlamydeous cohort shews further advance in economy than the sympetalous group now under consideration; for the gynæcium is often oligomerous in Rosales, the numbers 2 and 1 being of of relatively common occurrence. This condition is analagous to that which we found in comparing the Ericales with the Geraniales; and the analogy is curiously enhanced when we consider the evolutionary advance reflected in the zygomorphy found in the large rosalian order Leguminosæ.

The similarity in dehiscence and detailed structure of the anthers must be weighed in the same balance with the relative position of the ovary: and when we consider the extensive occurrence of epigyny throughout the Angiosperms, and the limited occurrence and obviously highly specialized nature of the ericalian anther character, the former seems to completely overbalance the latter in the investigation of this broad question of phylogeny. Epigyny, in fact, is one expression of broad general evolutionary progress, while this peculiarity in anther-structure cannot, *primâ facie*, be so regarded; and this if only for the reason afforded by the sum total of the species in which the two phenomena respectively occur throughout the Angiosperms, apart from any biological considerations. The nature of the anthers in Ericales must be regarded as an item of special importance only, so far as our present knowledge goes, in the absence of any general biological explanation therefore; it must thus be reduced to the same level with habit in the discussion of general affinities with other groups, although it may have considerable practical value in the diagnosis of the group itself. The anther-structure, like the habit, represents the special progress made by the group over and above the progress made on the broad general principle of economy, and does not reflect a general tendency external to the Ericales; it may, therefore, be accorded little or no weight in the search for external affinities for the group.

Such considerations as these seem to afford no little justification for urging that the Vaccinioideæ have an origin separate from that of the rest of the Ericales, and that consequently they should be separated from them in a natural system of classification. This origin, we have already hinted, may reasonably be sought in the ancestral stock represented by the Rosales; and we must suppose that the vaccinioidean line emerged from this stock before the appearance of the more advanced members of the Rosales, its determining principle being the fusion of petals to form a corolla-tube.

The position adopted in the foregoing may conveniently be summarized in the following diagram:—


Hypogynous
ERICALES
VACCINIOIDEÆ
line of sympetaly.
line of sympetaly.
GERANIALES
ROSALES
line of progressive economy
line of progressive economy and epigyny.
[Ranalian Ancestral Stock.]

The question arises, to what place are we to relegate the Vaccinioideæ in a natural system? This question, however, cannot be discussed fully until the other groups characterized by an inferior ovary (Inferæ) have been dealt with, and we must therefore postpone the matter accordingly.

PRIMULALES.

This cohort may be distinguished, like the Ericales, by the andrœcium; but, unlike the Ericales, the stamens are equal in number to the corolla segments and placed opposite to them. This anteposed arrangement is generally regarded as the indication of the presence of an outer alternating staminal whorl in the ancestral stock, and so the Primulales find a place in Pentacyclidæ in the one system, and Heteromeræ in the other. An outer whorl of "staminodes" is often present, and the temptation arises to regard these as representing the modified descendants of an ancestral outer whorl of stamens—not only in Primulales, but throughout the Angiosperms where these structures occur. Modern research,[1] however, which has been directed particularly to the members of this cohort, has thrown serious doubt upon the justification for such a conclusion, and has left quite open the general question of the true morphological nature of these so-called "staminodes." The discussion of this interesting question is beyond our present scope; it will suffice, perhaps, to say that no weight will be attached in these papers to the presence of these doubtful organs.

The stamens are typically epipetalous, with short filaments, and set at an appreciable height in the corolla-tube; it has been proved, further, that in certain Primulaceæ the petals and stamens have a common origin, the former being developed from the dorsal portions of the latter.[2] We may take the present opportunity to observe that epipetaly of the stamens is a phenomenon wide-spread throughout the Sympetalæ, and seems to follow naturally upon the evolution of the sympetalous corolla. The latter, we have seen, is correlated fundamentally with the principle of adaptation to insect visits; and epipetaly of the stamens may be regarded as a secondary economy tendency,[3] following upon and dependent upon sympetaly, This epipetaly is thus comparable with the other secondary tendencies to economy—oligomery of the andrœcium in zygomorphic forms, calyx-reduction, etc.,—to which we have drawn attention (*supra*, p. 116), and which we shall meet with in the higher sympetalous groups.

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[1] See, especially, Eichler, *Blüthendiagramme*.

[2] W. Pfeffer, *Zur Blüthenentwickelung der Primulaceen*, etc. Pringsheim's Jahrb. f. wiss. Bot. viii, 194.

[3] See *supra*, p. 82.

The invariable presence of a unilocular ovary distinguishes the Primulales sharply from the other two cohorts of Pentacyclidæ; the ovary is unlobed; and the number of carpels is further masked in the Primulaceæ and Myrsinaceæ by the condition of the style, which is undivided, capitate, with a simple stigma. In the Plumbaginaceæ, which include about 20% of the total number of species in the cohort, five styles are present, suggesting isomery of the gynæcium with the corolla.

The number of carpels in Primulaceæ and Myrsinaceæ has been made the subject of considerable attention, but research has failed hitherto to ascertain it at all definitely. The number five,—*i.e.*, isomery with the corolla—has appeared to be the most likely, and this has been hinted at by several considerations, such as the appearance of five or ten teeth in connection with the dehiscence of the capsule in many Primulaceæ; the appearance of five leaves in the place of an ovary in certain abnormal forms of *Primula*, and other phenomena in structure and development[1]; the presence of five styles in the allied Plumbaginaceæ, etc.

The detailed discussion of this question is outside our province; nor, indeed, is its solution of such fundamental importance for our purpose as at first sight may appear. In the other two cohorts of Pentacyclidæ the ovary is multilocular, and the carpel-number is determinate; but in the Primulales the flower differs so essentially, apart from the gynæcium, from those of Ericales and Ebenales, that there can be little question of close affinity between the two; the comparative structure of the ovary thus loses much of its significance. We have, in fact, to search in a direction different from that of the ericalian stock for the ancestry of the Primulales; not only the Sympetalæ as a whole, but the subordinate group of Pentacyclidæ also, we shall find, are very probably polyphyletic in origin.

In Myrsinaceæ and Primulaceæ the ovary is usually multiovulate, although a distinct tendency to reduction in the number of ovules is observable; and in Myrsinaceæ all but one usually abort at maturity, and the fruit is one-seeded. In Plumbaginaceæ the unilocular ovary contains invariably but one ovule, placed basally. The ovules in the first two natural orders are borne upon a so-called "free-central" placenta, a structure continuous with the floral axis and projecting into the ovary chamber.

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[1] See T. G. Hill. "On Variation in the Flowers of certain species of *Primula*." Ann. Bot., XVI (1902), p. 317, where relative literature is cited.

As in the Ericales, traces of polypetaly remain in the Primulales. The petals are free in the genus *Embelia* of Myrsinaceæ, comprising some sixty species, and in some species of *Myrsine* : of the Plumbaginaceæ an extensive section (Staticeæ) is distinguished by a polypetalous or subpolypetalous corolla.

We may now approach the question of the archichlamydeous origin of the Primulales; and our attention seems directed naturally to the Centrospermæ as representing the stock from which this cohort may reasonably have been derived. The Centrospermæ include, approximately speaking, the Curvembryeæ of Bentham and Hooker—a cohort of Incompletæ—together with the Aizoaceæ and the heterochlamydeous Portulacaceæ and Caryophyllaceæ; the last named natural order includes about 40% of the species in the cohort, and the Chenopodiaceæ with Amarantaceæ, about 30%.

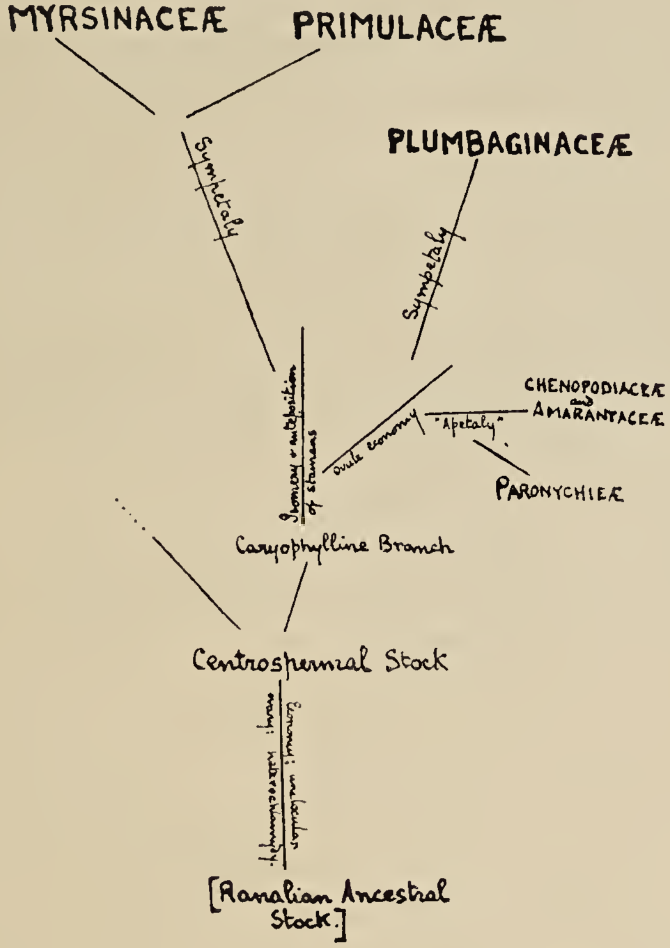
In the Caryophyllaceæ, which may be taken as representative of the main centrospermal stock, the stamens are usually borne in two whorls, each isomerous with the corolla, and with the members of the outer whorl placed opposite to the petals. There is, however, an unmistakeable tendency to reduction in the andrœcium and this tendency is realized in the Centrospermæ and Amarantaceæ, in which the stamens are typically isomerous with, and anteposed to, the corolla-segments.

The carpels, again, are typically isomerous with the corolla, displaying at the same time a tendency to oligomery. The ovary is unilocular, the ovules being borne upon a free-central placenta formed, apparently, by the degradation of septa. In the Chenopodiaceæ and Amarantaceæ the ovary is unilocular, and contains a solitary basal ovule.

The caryophyllaceous flower is typically heterochlamydeous, like that of the stocks represented by Geraniales and Rosales respectively. The Chenopodiaceæ and Amarantaceæ appear to represent a tributary line determined by loss of the heterochlamydeous character.

The derivation of the Primulales from the alliance briefly sketched above is not difficult of conception. Probable lines of evolution are indicated in the annexed diagram.

Starting with what may be designated the caryophylline branch of the centrospermal stock, represented by Caryophyllaceæ and Portulacaceæ, the main progressive line is that of economy in the andrœcium; this we should reasonably expect from the aspect of our fundamental principles. At a relatively early stage a side-branch emerges, determined by a tendency to the uniovulate condition. Sympetaly arising from the former (main) line leads to the Primulaceæ and Myrsinaceæ: sympetaly arising from the latter (branch) line leads to the Plumbaginaceæ.


MYRSINACEÆ
PRIMULACEÆ
Sympetaly
PLUMBAGINACEÆ
Sympetaly
Isomery & antepositión of stamens
ovule economy
"Apetaly"
CHENOPODIACEÆ and AMARANTACEÆ
PARONYCHIEÆ
Caryophylline Branch
Centrospermal Stock
Economy; unilocular ovary; heterochlamydy.
[Ranalian Ancestral Stock.]

A faint trace of a tendency to epigyny appears in the caryophylline stock,—e.g., *Portulaca*, *Beta*; this is reflected in the Primulales in *Mæsa*, *Glaux*, and *Samolus*. Unlike the Vaccinioideæ, derived, we suggested, from a plexus characterized by a definite and general tendency to epigyny, the Primulales have made no advance in this direction, but have retained the hypogynous arrangement in the great majority of their species.

General progressive adaptation to insect visits among the Primulales has halted, broadly speaking, at sympetaly; zygomorphy is unknown, except in the aberrant genus *Coris*, comprising but one or two species, occurring in the Mediterranean region. Special adaptation is found in the form of heterostyly—a phenomenon which has been familiarized by the well-known example of *Primula*; but how far this is so general a feature of the cohort as to be regarded as a distinctive character needs investigation.

EBENALES.

This group consists almost entirely of tropical trees; the andrœcium, comprising typically at least two whorls, and often more, entitles it to a place in the Pentacyclidæ. The stamens are not infrequently indefinite in number, and this character is constant for the Symplocaceæ; in these cases the stamens are often united in groups. In Styracaceæ the stamens are usually more numerous than the corolla-segments, but are uniseriate in arrangement. Isomery of the andrœcium is frequent in the Sapotaceæ, the stamens being placed opposite to the petals; very rarely the stamens equal the petals in number and alternate with them—e.g., *Maba* (Ebenaceæ)

The stamens are hypogynous in some Ebenaceæ, but are generally inserted at the base of the corolla in that natural order and in Styracaceæ and Symplocaceæ. In Sapotaceæ the stamens are epipetalous on the corolla-tube.

The gynæcium is typically isomerous with the corolla, although the number of carpels may be more or less indefinite, on the one hand, or two only, on the other; the ovary is usually multilocular. In Styracaceæ and Symplocaceæ the ovules are few in each loculus; in Ebenaceæ the number of two per loculus is not exceeded, and in Sapotaceæ each loculus is uniovulate.

The petals are free or almost so in the Symplocaceæ; but in the other orders sympetaly is fully established. The flowers are regular throughout the cohort; there is no tendency to zygomorphy. Conspicuousness is attained by the more or less close clustering of relatively small flowers in axillary inflorescences.

In view of its essential characters, this cohort would appear to share a common ancestry with the archichlamydean Parietales. Engler has included a large number of natural orders in the latter group, which comprises, broadly, the Guttiferales and Passiflorales of Bentham and Hooker, together with certain of their "Parietales." and Caryophyllinæ.[1]

We have already drawn attention to Engler's Parietales as reflecting, first, what we have designated the secondary branching tendency,[2] and second, the tendency to epigyny[3]; and the expression of both these is clearly observable in the Ebenales. The polypetalous cohort is characterized by an indefinite andrœcium, coupled with a tendency to oligomery, in most of the natural orders, and also to miscellaneous cohesion, as in Symplocaceæ. A glance at the table on p. 146 will suffice to shew that this tendency to economy is parallelled in the Ebenales, the Sapotaceæ seeming to represent its highest expression, analogous to *e.g.*, the Violaceæ and Passifloraceæ of Parietales.

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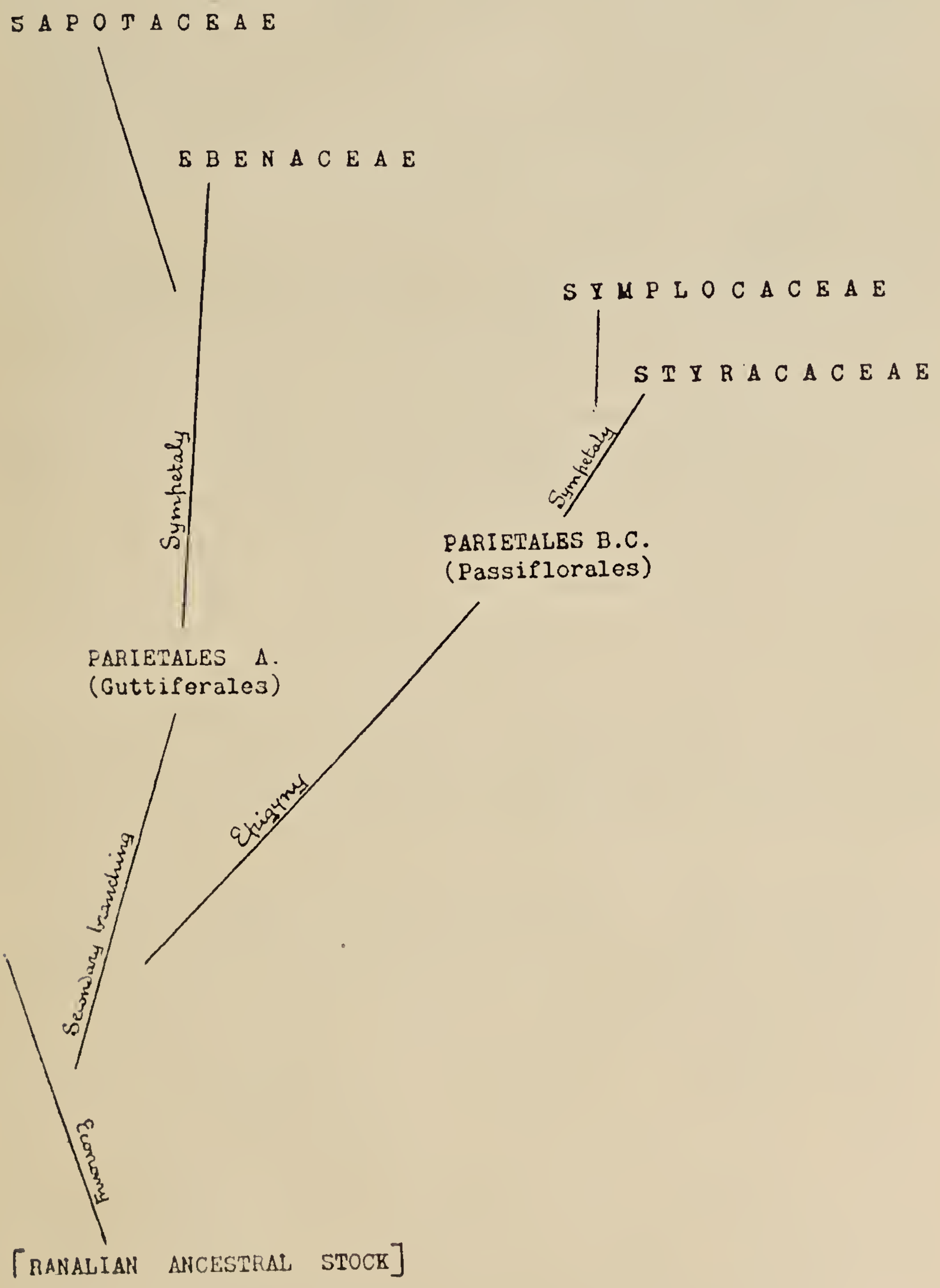
[1] See Willis. "Flowering Plants and Ferns." pp. 129, 130, 132.

[2] *Supra*, pp. 80, 111. [3] *Supra*, p. 116.



The carpel numbers are similar for the two cohorts; but in the Parietales a unilocular ovary is a characteristic feature. The multilocular condition is, however, represented in the extensive cohort Guttiferales of Bentham and Hooker, included in Engler's group A of Parietales. The Ebenales appear to be more specialized in the character of ovule number, although, as we have seen, the multiovulate ovary is not rarely represented.

Lastly, the parietalian tendency to epigyny is reflected in the Styracaceæ and Symplocaceæ; and the similarity between the floral characters, *e.g.*, of the latter order and of the Loasaceæ affords a striking illustration of the parallelism between the cohorts. The essential difference lies in the one-chambered ovary of the higher Parietales, and the progress to this condition seems to be the key-note of special evolutionary development within that group. This element is wanting in the Ebenales; they may thus represent the sympetalous descendants of the plexus typified in the Guttiferales of Bentham and Hooker—descendants which have, in some cases, adopted the tendency to epigyny traceable in other members of the ancestral stock. The possible lines of origin of the Ebenales from the parietalian stock is roughly indicated in the above diagram

In conclusion we may summarize the Pentacyclidæ as a polyphyletic group originating by the grafting of sympetaly upon at least three archichlamydeous stocks, *viz.*—the geranial, the centrospermal, and the parietalian (see diagram, p. 159.) Sympetaly appeared moreover, at a relatively early stage in the progression of each stock, so that the working of the *primary* tendency to economy is clearly traceable within each cohort of the sympetalous group. The polypetaly, or sub-polypetaly, of not a few members of the latter afford evidence of its ancestry; while epipetaly of the stamens, expressive of a *secondary* tendency to economy of material following upon the formation of a corolla-tube, is observable within each of the three cohorts. As regards the higher general adaptations to insect visits, conspicuousness is attained chiefly by the clustering of relatively small flowers; the clusters, however, are never so dense or so specialized as to bear comparison in point of significance with those of Umbelliferæ or Compositæ: zygomorphy is a very rare feature. The absence among the Pentacyclidæ of these two elements,—close aggregation and zygomorphy—coupled with the prevalent pleiomery of the andrœcium and the remnants of polypetaly, lead us to regard them as expressive of the first steps taken by different archichlamydeous stocks in the direction of sympetaly, before their primary tendencies to economy were at all fully realized.

In these circumstances we are not surprised to find isolated cases of epigyny or semi-epigyny in Primulales and Ebenales derived, as we have suggested, from stocks in which a tendency to epigyny is displayed—*viz.*, the centrospermal and the parietalian (see diagram above). The geranial stock, however, shews no such tendency, and for this reason we are led to doubt the propriety of associating the Vaccinoideæ with the descendants of this stock—*i.e.*, with the Ericales. The vaccinioideæ may, not impossibly, represent the progeny of a fourth stock, the rosalian: we shall return to this point later.

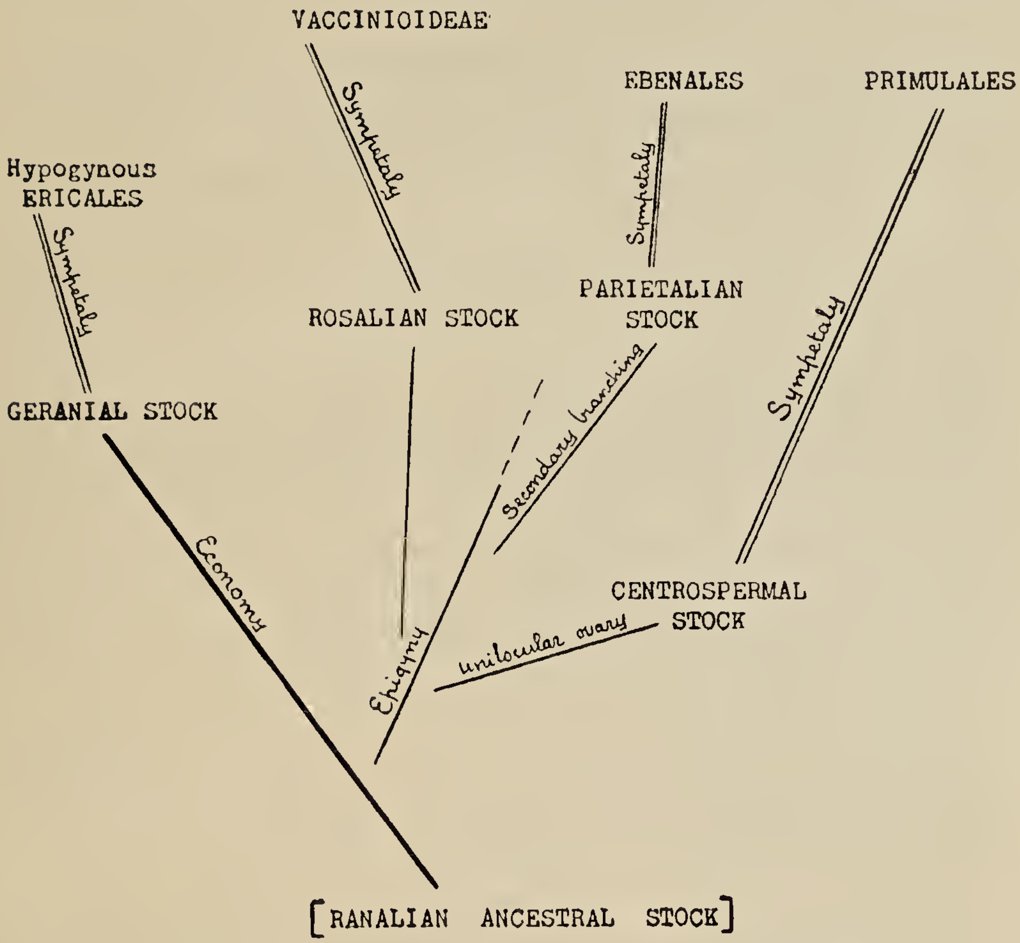


Diagram illustrating the possible origin of the Pentacyclidæ. The double lines indicate the polyphyletic nature of this origin.

We may add finally that, the specialized nature of the habit and habitat of many of the Pentacyclidæ suggests a *primâ facie* presumption that its constituent natural groups represent terminal points upon their several lines of evolutionary advance; this presumption, we shall find, will be justified to a considerable extent in the sequel.

(*to be continued*).

ON THE DETECTION OF MALTOSE IN THE TISSUES OF CERTAIN ANGIOSPERMS.

By S. Mangham, B.A.

Formerly Exhibitioner, Emmanuel College, Cambridge and University Frank Smart Student in Botany.

[Figs. 1—4].

In studying sugars from the point of view of plant physiology, certain practical difficulties are encountered which hinder progress in the knowledge of the parts played by these compounds in the vital activities of the plant. These difficulties are partly inherent in the nature of the investigations themselves, especially when these aim at determining by microchemical methods the nature and distribution of the sugars present in plant tissues under various conditions.

The small size of a plant cell is a formidable obstacle to a satisfactory investigation of its contained sugar, and although the aid of a fine capillary tube has been invoked by some investigators[1] to withdraw some of the contents of individual cells for subsequent examination, it is as a rule necessary to apply the test in use simultaneously to a number of cells, such as are contained in a section of the tissue. Needless to say satisfactory sections are not always readily obtainable.

It has been customary to employ Fehling's solution as a microchemical test for sugars in the tissues of plants. But this reagent has several disadvantages of which the more important are (1) that it does not give a precipitate with some of the sugars known to occur in plants, *e.g.*, cane sugar, (2) that it also reacts with other bodies than sugars which may be present in the cells, *e.g.*, tannin, and (3) that whatever the substance may be which reduces the solution, the resulting precipitate is always the same. Accordingly it is not possible by the mere application of Fehling's solution to determine whether free sugar alone is present, still less to distinguish between the sugars which effect reduction.

Apart from the inadequacy of the solution as a chemical reagent certain other disadvantages are met with in applying it practically.

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[1] Stopes, M. C. C., and Fujii, K. "The nutritive relations of the surrounding tissues to the Archegonia in Gymnosperms." Bot. Centralbl., Beihefte XX., Abth. 1, 1906, p. 6.

The tissues become very much softened by the action of the hot alkaline fluid and it is then very difficult—often impossible—to remount them.

As the reagent is an aqueous one, little resistance is offered to diffusion of the sugars from the cells, and so the distribution of the precipitate may not be a true indication of the previous distribution of reducing sugars.

The crystallising of the liquid as the water evaporates entails a rapid remounting (when this is possible) and so makes comparative work inconvenient and tedious.

Moreover the minute granules of copper oxide precipitated are not always easily observable.

To a certain extent these difficulties are overcome in a method introduced by Senft.[1] This is based upon Fischer's discovery of the formation of yellow crystalline osazones when sugars containing the aldehyde or ketone group are treated with phenylhydrazine in slightly acid solution. These osazones are easily visible, are insoluble in cold water, glycerine and dilute caustic potash, and in some degree are characteristic for the sugars from which they are produced.

The reagent is made up, not with water but with glycerine,[2] in which sugar is very much less soluble, and which does not evaporate and allow crystallisation of the reagent.

Phenylhydrazine hydrochloride and sodium acetate are dissolved separately in about ten times their weight of glycerine. Warming is advisable in order to dissolve the reagents satisfactorily, and the liquids should be filtered once or twice before use.

In applying the method to examine the distribution of sugars a drop of each liquid is put on a glass slide and mixed with a mounted needle, and a section of the tissue is then cut and laid in the reagent. The section, which must of course be more than one cell thick, is covered with a glass slip, and the preparation is either left for future examination or is placed in an oven heated by a water-jacket, where it may be left for any desired time.

Without heating, the reaction is slow and uncertain, and in comparative work it is preferable to heat the preparations and so accelerate the formation of osazones, although by so doing the chances of diffusion occurring are increased.

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[1] Senft, E, "Über den microchemischen Zuckernachweis durch essigsaures Phenylhydrazin." Sitz. d. k. Akad. d. Wiss. in Wien, Mathem.-Naturw. Kl., Bd. CXIII., Abth., 1, 1904, pp. 3—28; Bot. Centralbl., 1904, pp. 28, 29.

[2] Plasmolysis is thus produced, but appears to be of little consequence in actual practice. In any case comparison of structure can easily be made with fresh material.

After cooling, the slides can be left several weeks or even months without harming the sections, provided air is not allowed to come into contact with the tissues. If it is desired to remount the sections they can easily be removed, washed in cold water, if necessary cleared by placing in 2% caustic potash for a few minutes and re-washing in water containing a drop or two of acetic acid, and then taken up by one or two stages to pure glycerine. It is possible to use aqueous stains to some extent, but alcoholic solutions cannot be employed as the osazones are soluble in alcohol. Air bubbles can be removed by exhausting under the receiver of an air-pump. Finally the preparations can be closed by applying a mixture of gum mastic and paraffin wax to the edges of the cover-slip.[1]

In order to become acquainted with the action of the reagent drops of solutions of pure sugars can be employed, the strengths of the solutions and the duration of heating being varied

Senft himself tried such experiments with very strong solutions, using equal parts of water and sugar[2]. But it is preferable to work with much weaker solutions, such as probably exist in the plant-cell which is often plasmolysed by a 5% solution.

When simply mixed with the reagent and left unheated Senft found that his strong solution of levulose yielded the osazone within a few hours, numerous sheaf-like clusters and spherical aggregates of needle-shaped crystals being formed. In the case of dextrose, however, at the end of twenty-four hours no crystals had formed, though the preparation shewed a lemon-yellow colour. On the third day a few small spherical crystal aggregates appeared. With both levulose and dextrose the amount of osazone produced increased for a few days. Cane sugar was found to give no osazone crystals in the cold even at the end of five days.

In other experiments drops of the strong solutions were heated with the reagent for periods varying from five minutes to half-an-hour and the changes produced were observed on removing the slides from the water-bath. Levulose, after five minutes, exhibited an orange-yellow colouration the depth of which increased as the heating was prolonged. At the end of half-an-hour the slide was removed to cool whereupon it very quickly yielded an abundant crop of extremely large sheaves and bundles of osazone crystals.

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[1] For a description of this convenient method of closing glycerine preparations, cf. Thomas, H. H., New Phytologist, March, 1911, pp. 105, 106.

[2] L.c., p. 10.

Dextrose behaved in very much the same manner, but the production of crystals was less rapid and the amount smaller.

Cane sugar, after being heated for ten minutes, shewed a slight lemon-yellow colouration, which had changed to orange-yellow at the end of another five minutes in the water-bath. On allowing the preparation to cool after having been heated for half-an-hour, Senft found that a copious supply of sheaf-like crystal clusters was soon yielded, a result which he attributed to the inversion of the cane-sugar by the action of the hot reagent, with the production of levulose and dextrose.

He does not appear to have employed maltose at all in this portion of his work. Crystals of maltose phenylosazone are, however, shewn in his figures, illustrating the results subsequently obtained with *Ginkgo biloba*, *Daucus Carota* and *Elodea canadensis.*

In repeating these experiments with solutions of levulose and dextrose of strengths varying from ·5% to 10%, while obtaining the same general results after heating for half-an-hour at 100°C, I have often noticed that levulose shews a preference for the large radiating or sheaf-like form of crystal grouping, while dextrose more often forms smaller and more spherical aggregates of crystals. With 5% or 10% levulose the sheaves of crystals branch repeatedly and rather resemble the patterns produced by frost on window panes, a result rarely given by dextrose. The actual forms obtained vary with the strength of the solutions and may, perhaps, depend also upon other factors, but the distinction holds good for moderately weak solutions in a general way (Figs. 1 and 2).

With regard to cane-sugar while stronger solutions do undergo a certain amount of inversion after prolonged heating, in the case of weaker solutions this inversion appears so small as almost to be negligible. Working with solutions of "Cane sugar," I found that osazone crystals were obtained some time after cooling when a 10% solution had been heated for an hour, but that a 5% solution gave no crystals during the succeeding two or three days. Subsequently I repeated the experiments with drops of a 5% solution of "Cane sugar, puriss." After an hour's heating no crystals had appeared at the end of five days, although numerous minute yellow drops of liquid had formed.

After heating for an hour-and-a-half only yellow drops were

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[1] L.c., pl. II., figs. 8-11.

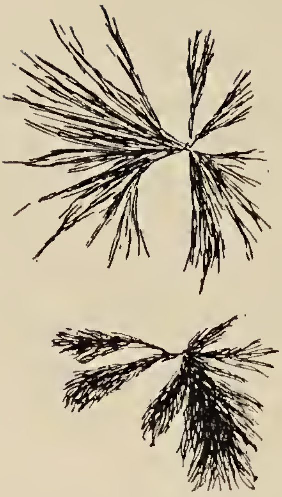

Fig. 1.

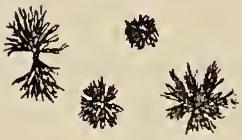

Fig. 2.

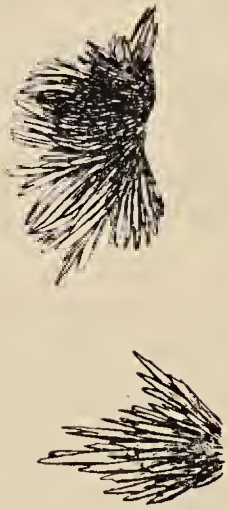

Fig. 3.

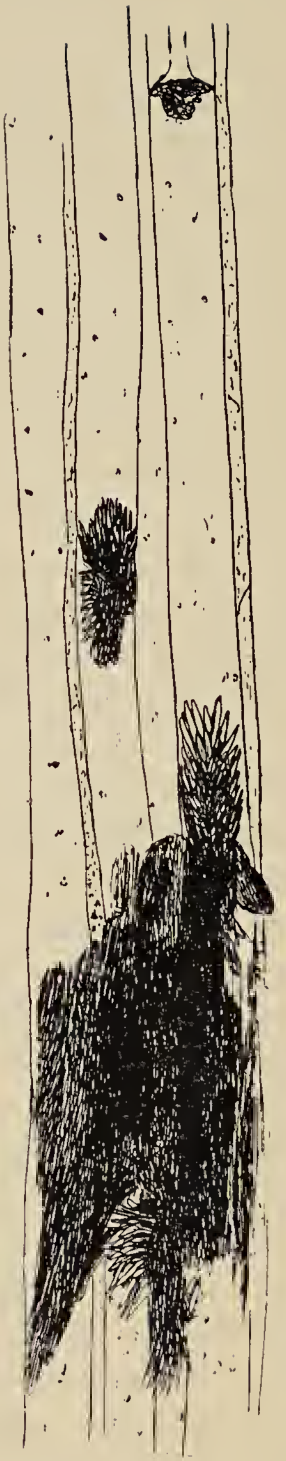

Fig. 4.

Fig. 1. Osazone from 2·5% solution of Levulose. × about 250,

Fig. 2. Osazone from 2·5% solution of Dextrose. × about 250.

Fig. 3. Groups of crystals of maltose phenylosazone from *Helianthus annuus.* × about 250.

Fig. 4. Portion of the phloem of *Cucurbita Pepo* showing the presence of crystals of maltose phenylosazone inside sieve-tubes. × about 250.

visible at the end of five days, while with two hours' heating there were signs of the formation of crystals from a yellow, syrupy liquid five days later.

After six months the preparations were re-examined and a few cystals had then been formed. It therefore seems doubtful if Senft's reagent is a very reliable one for the location of moderately weak solutions of cane sugar in plant-tissues, for the prolonged heating required to effect inversion promotes diffusion of the cell-contents. Quantitative results are therefore scarcely obtainable in this way.

On the other hand the reagent forms osazones with extremely dilute solutions of levulose and dextrose[1] and so for these sugars provides a very delicate test.

By employing carefully purified methylphenylhydrazine Grafe was able to distinguish between levulose and dextrose since this reagent only forms crystalline osazones with sugars containing the ketone group. These crystals were of a yellow-brown colour and quite distinct from those obtained with Senft's reagent. With cane sugar Grafe found that his reagent produced the characteristic levulose methylphenylosazone after heating for an hour-and-a-half.

Maltose yields a phenylosazone of a very definite character. Weak solutions, 1% to 5%, give after an hour's heating dark yellow drops of liquid resembling treacle or "Golden Syrup." From these drops crystals of the osazone may form after some considerable interval—often several weeks. In colour these are a clear, lemon-yellow—not the golden yellow of the osazone formed from levulose or dextrose. The actual crystals are lamellate and very much larger than the fine, acicular crystals yielded by levulose and dextrose. They form rosettes or they may occur in dense, almost opaque masses which are recognisable with the naked eye. At the edge of such masses the typical maltose phenylosazone crystals can usually be made out (Figs. 3 and 4). Once formed the crystals are fairly unmistakable, but the apparent uncertainty of their production from the dark yellow syrup and their habit of forming in large isolated masses renders the exact location of maltose in plant-tissues rather difficult.

In the course of an experimental investigation of the paths of translocation of sugars in plants, I have observed the occurrence of these crystals in longitudinal sections of the veins of various starch-forming dicotyledonous leaves, viz. *Helianthus annuus*, *Cucurbita Pepo*, *Phaseolus cerasiflorus*, *Physalis Alkekengi*, and in the stem of *Urtica dioica*. The crystals occur in detached, dense masses in the assimilating cells, the phloem of the vascular bundles and in the nerve parenchyma. They are very obvious when viewed through the microscope as opaque objects, owing to their light yellow colour.

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[1] ·015% according to Grafe.

[2] Grafe, V. "Studien über den mikrochemischen Nachweis verschiedener Zuckerarten in den Pflanzengewebe mittels der Phenylhydrazinmethode." Sitz. d. k. Akad. d. Wiss. in Wien, Mathem.-Naturw. kc., Bd. CXIV., Abth. 1, 1905, 115-128.

In connection with various anatomical considerations and experimental results, which have indicated that sugars are translocated from the leaf in the sieve-tubes,[1] it is interesting to note the very close association of these crystal masses with sieve-tubes. In such cases the sieve-tubes themselves are often lined with an orange-coloured liquid like that from which the crystals of maltose phenylosazome are formed. The masses of crystals appearing at intervals in close contact with the sieve-tubes seem to have been produced from some of the syrupy contents of the sieve-tubes. That crystals do not regularly appear within the sieve-tubes may be due to the confined space, for in *Cucurbita*,[2] where the diameter of these elements is large, crystals have been observed inside them (Fig. 4). Thus direct evidence is furnished of the presence of maltose in the sieve-tubes of the *Cucurbita* under conditions when translocation was known to be going on.

The close association of the crystals with the sieve-tubes in the other plants, and the presence within them of the yellow syrup, suggest that in these cases also maltose travels as such in the sieve-tubes.[3] Doubtless it becomes hydrolised, *en route*, by enzymes present in the sieve-tubes or excreted by the companion cells, as is suggested by the fact that while the distal ends of the sieve-tubes often contain only the yellow syrup, towards the proximal ends a more definitely crystalline content is to be observed. This is particularly the case with *Helianthus annuus*, where the crystals resemble those given by dextrose, although this sugar is not necessarily present only as the result of the hydrolysis of maltose.

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[1] cf. Mangham, S. "The translocation of carbohydrates in plants." Science Progress, Oct. 1910, Jan. 1911.

[2] The leaf had been darkened for some days.

[3] cf. Brown and Morris. "A contribution to the Chemistry and Physiology of Foliage Leaves." Journ. Chem. Soc., 1893, p. 673.

FURTHER INVESTIGATIONS OF METHODS OF REPRODUCTION IN THE SAPROLEGNIACEÆ,

By A. Eckley Lechmere.

[With Six Pages of Figures.]

PART I.

Introduction.

HAVING had occasion a short time ago to undertake an investigation of the life history of a species of *Saprolegnia* (11) from the point of view of observing any alterations produced by growth under various cultural conditions, I was naturally interested when an opportunity arose of comparing the results already published with those which might be obtained from the same species found in another locality.

The present species is one of two species found in a sample of water collected from a pond in the Forest of St. Germain on the occasion of an excursion there for the purpose of collecting specimens of Algæ and Fungi for the Museum. The specimens collected were brought back to the Laboratoire de Cryptogamie for investigation.

In one sample of water, containing many Algæ and Protozoa some very good examples of oocysts of some species of *Saprolegnia* were found.

Many of the oocysts showed very clear cases of fecundation, the antheridial tubes being clearly seen penetrating the oocyst and terminating in connection with the oospheres.

As there seemed to be a fair amount of the *Saprolegnia* present, I took the opportunity of again obtaining the species in pure culture.

Method of Isolation and Culture. The isolation of the *Saprolegnia* from the mixture of Algæ was carried out by means of small pieces of coagulated albumen (white of egg) floated on the surface of the water contained in a glass vessel, in which had been placed a selected portion of the mixture of Algæ and *Saprolegnia* containing as large a quantity as possible of *Saprolegnia* filaments.

By this means, in the course of a few days, many of the pieces of egg showed a fringe of hyphæ having the appearance typical of the Saprolegniaceæ. Several cases were found showing formation of sporocysts, The pieces bearing mycelia were isolated and well washed in fresh water and transferred to Petri dishes containing distilled water.

On examination of the series of mycelia isolated in this manner, two distinct species were found to be present; each of these was then isolated into pure culture by the following method. A small piece of the mycelium was teased off with fine needles and transferred to meat extract gelatine in Petri dishes. Full details of this method are given in the other paper.

In each case the fungus grew very rapidly on this medium, but at the same time produced very vigorous liquefaction, which enabled the protozoa and bacteria to spread to the edge, and so rendered isolation of hyphæ free from bacteria difficult.

To overcome this point, the plates were tilted at an angle of 60°, the direction of the vertical being marked on the back of the dish by an arrow drawn in wax so that the plate could always be replaced in the same position. In this way all the bacteria, etc., were carried to the lower part of the plate culture, leaving a fringe of hyphæ perfectly free from organisms growing towards the upper portion. Other plates were inoculated with small fragments of hyphæ taken from the extreme upper edge of a two days' growth, and very soon the cultures were obtained free from organisms.

Growth on the gelatine medium is always entirely vegetative, so, in order to follow the life-history of these two species, a series of cultures in each case was made on white of egg in distilled water, sterilized Petri dishes being used throughout.

As a result of the previous investigation, white of egg was found to be by far the most convenient medium with which to work.

The stock of albumen is easily prepared by placing small slices of the white of a hard-boiled egg in test-tubes containing water. These tubes can then be sterilized in an autoclave at 120°C for twenty minutes, and so preserved for future use. For the purpose of the cultures, small pieces of albumen can be removed from these slices by means of a thick platinum needle and transferred to the Petri dishes containing distilled water.

After two to three days' growth on the albumen, a fairly dense fringe of hyphæ is developed, and formation of sporocysts commences, at this stage the water is changed every other day to keep the cultures fresh.

After a fairly vigorous mycelium had been developed several cultures were allowed to remain without changing the water, to induce formation of gemmæ. From these various cultures small pieces of the mycelium were teased off and mounted as hanging drop cultures to follow in detail the formation and discharge of the sporocysts and the formation of oocysts.

Examination of the First Species.

Species I. This species in general appearance resembled very closely the species described in the previous paper, the chief point of difference being the tendency to form oocysts at a very early stage. The oocysts were often formed soon after sporocyst formation had commenced, instead of occurring as is usually the case at a later stage, when the formation of sporocysts has been continued for some time.

In this feature it shows a marked contrast to the former species, which could not be induced to form sexual organs under any conditions, but in all the other features it shows a very close resemblance.

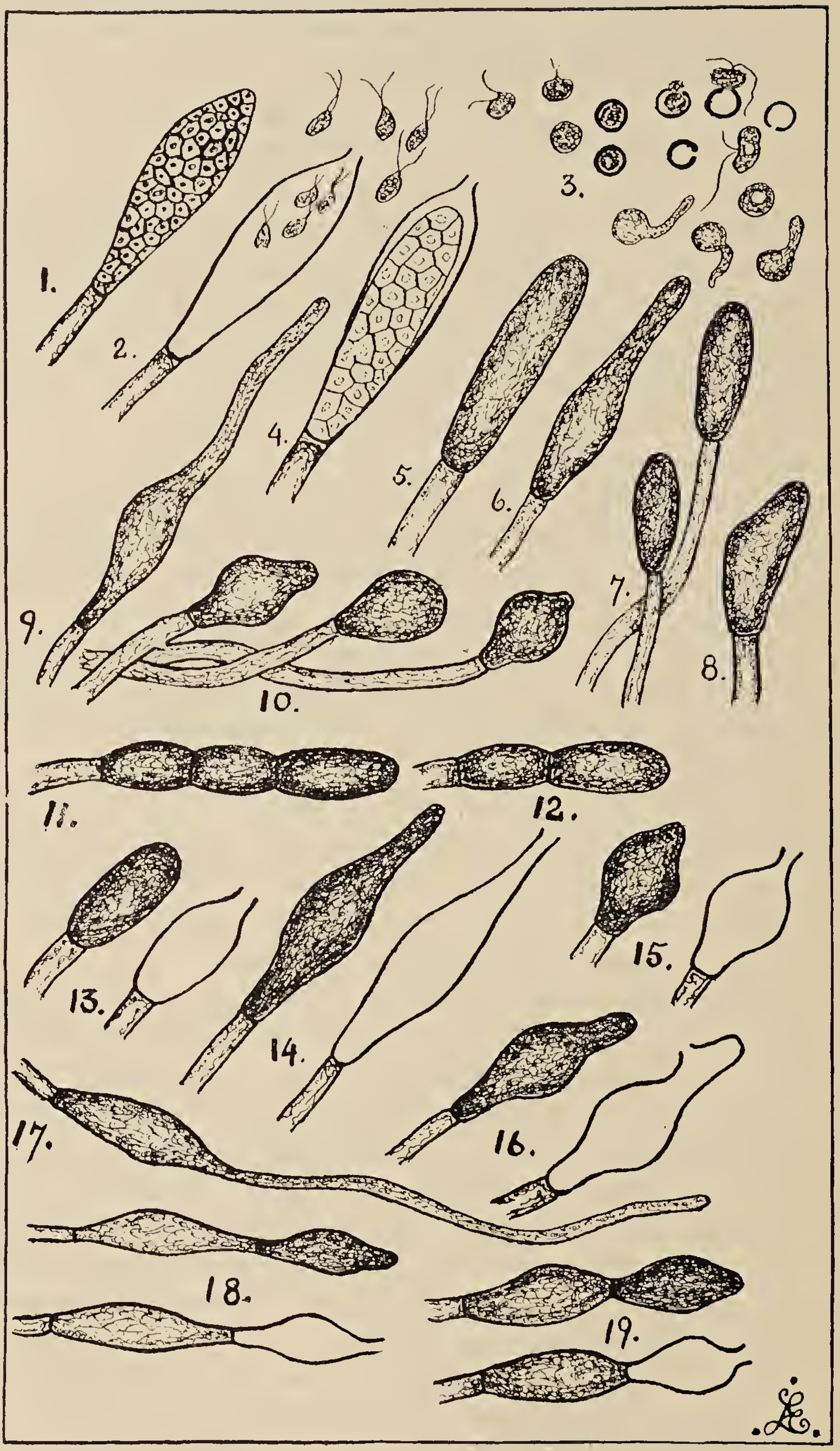
Typical life-history of Species I. The following is the account of the life-history of this species as shown by numerous hanging drop cultures and small pieces frequently teased off the cultures in the Petri dishes.

The mycelium at first consists of slender cœnocytic hyphæ showing a tendency for the protoplasm to condense at the apex, causing swelling of the hyphæ. Very soon growth is arrested by the formation of a terminal club-shaped sporocyst containing the zoospores arranged in several rows (p. 170, fig. 1).

The zoospores are formed in the typical manner and are discharged in the motile state through a short terminal process (p. 170, fig. 2). After discharge, they swarm actively for a short time before coming to rest and encysting, in which state they rest for a period of eight to twenty-four hours. After the resting-period is completed the contents of the spore protrudes as a small bud and soon the whole contents is discharged through the small aperture in the spore wall, and then enters upon the second motile stage, leaving the empty spore case behind (p. 170, fig. 3). Numerous empty cases are seen in the hanging drop cultures.

The same difference was noticed in the form of the two kinds of zoospores, as already noted (loc. cit., p. 313).

After the discharge of the zoospores, a new sporocyst grows up inside the wall of the one first formed; numerous cases showing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this condition were found in the cultures, thus indicating the genus *Saprolognia* (p. 170, fig. 4).

The next step in the life-history is the formation of oocysts; these were formed at a very early stage, and commenced as terminal swellings on the hyphæ (p. 172, fig. 1).

At first the oocysts appear evenly filled with granular protoplasm, but the contents soon begin to segregate into several separate masses, which later become the oospheres (p. 172, figs. 12 and 13). This process has already been fully described by previous workers under the title of "balling of the ova."

The number of oospheres thus produced, varies from four to eight, and, in some cases, twelve (p. 172, figs. 2, 13, 14 and 15.)

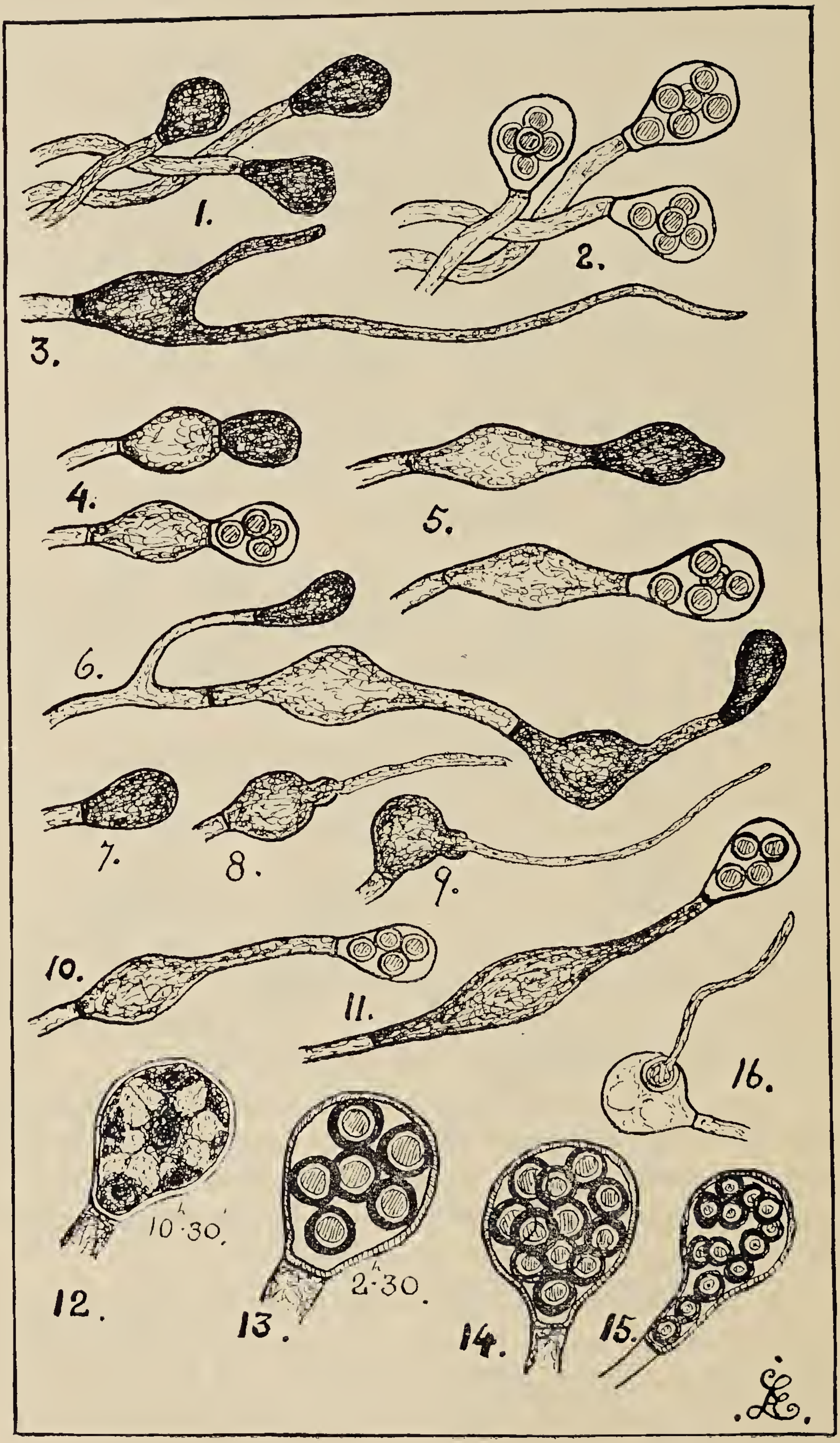
All stages can be observed in hanging drop cultures, and it is generally during the process of "balling" that the antheridial branch is seen to become applied to the wall of the oocyst (p. 175, figs. 6—9).

When the "balling" is complete, the oospheres are seen clearly defined with a membrane, and in several cases antheridial tubes were observed penetrating the wall of the oocyst and terminating in connection with the oospheres.

The formation of the *Antherocyst* in this species was a point of great interest, as it showed a variety of forms. The typical case seemed to be where it arose from an adjacent branch of the main hyphæ and forms a more or less branching net-work round the oocyst (p. 175, figs. 4—11), but cases of almost equal frequency were noted where both the oocyst and antherocyst arises from lateral branches of the same hypha (p. 175, figs. 12—16). A third method was noted where the antherocyst was derived from the hypha actually bearing the oocyst (p. 175, figs. 17 and 18).

Cases of fecundation, or at least cases of the undoubted presence of the antherocyst, were chiefly found in the young and vigorous cultures; later on, the older cultures seemed to lose the property of producing the antherocysts. In these cases the oocysts produced the oospores parthenogenetically.

In the older cultures, where nearly all the oocysts appeared to be parthenogenetic, the number of oospores was noticed to be greater, the average being eight or twelve (p. 172, figs. 14 and 15), whereas in those first formed it is usually four or six. The dimensions of the oospores remain the same in each case, the average diameter being 22μ.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In the formation of both sporocysts and oocysts, many cases were observed where the process of formation had been arrested at an early stage, owing to unfavourable conditions of the cultures. This results in the formation of a resting sporocyst, or gemma (p. 172, figs. 5—9).

As in the case of the last species, the size and form of the gemmæ varied very much, also the method of germination.

In both forms of gemmæ, *i.e.*, resting sporocysts and resting oocysts, cases have been observed where the germination was entirely vegetative (p. 170, fig. 17 and p. 172, figs. 3, 8 and 9). The more usual method of germination on transference to a fresh water culture is to continue the process of sporocyst or oocyst formation.

In the case of gemmæ developing into sporocysts, two methods are found to occur. In the first place, the whole gemma may become directly transformed into a sporocyst with a tubular process through which zoospores escape (p. 170, figs. 13—16).

In the second case, which, in this species, was the most general, the gemma develops a short tube terminating in a club-shaped swelling which develops directly into a secondary sporocyst discharging motile zoospores (p. 170, figs. 18 and 19).

Cases have been observed where the germ-tube terminates in a secondary gemma, and one case is figured where the secondary gemma has germinated and in its turn produced a tertiary gemma (p. 172, fig. 6).

In the case of the gemmæ which give rise to oocysts, a secondary oocyst is invariably formed which may be directly attached to the gemma from which it arose (p. 172, fig. 4), or it may be formed as a terminal swelling at the end of a germ-tube in exactly the same way as the secondary sporocysts formed in the same position (p. 172, figs. 5, 10 and 11). In structure and general appearance the two forms of gemmæ are identical, and in the case of the forms which produce a germ-tube terminating in a swelling, it is only by watching the development of the swelling that the fate can be determined.

VARIATIONS OF THE LIFE-HISTORY.

The following variations of the typical life-cycle have been noticed in various older cultures.

Multiple sporocysts. In some of the older cultures a few cases were found of multiple sporocysts in the resting condition, *i.e* resembling a chain of gemmæ. But cases showing this condition were not nearly so numerous as with the former species (p. 170, figs. 11 and 12).

Laterally formed sporocysts. A few cases were found where a sporocyst arose as a lateral branch below the one already discharged. The case figured (p. 175, fig. 1) shows this condition and a new sporocyst growing up within the wall of the first-formed sporocyst, thus apparently combining the *Achlya* and *Saprolegnia*-type of formation.

The Aplanes type. In several hanging drop cultures of a few days' growth, cases occurred in which the spores had failed to discharge and had germinated *in situ* (p. 175, fig. 2).

Dictyosporocyst. In many cases of the gemmæ developing directly into sporocysts with long tubular processes, the majority of spores failed to discharge, so the second motile stage takes place within the sporocyst and after the escape of the zoospores the empty cases remain in the sporocyst (p. 175, fig. 3).

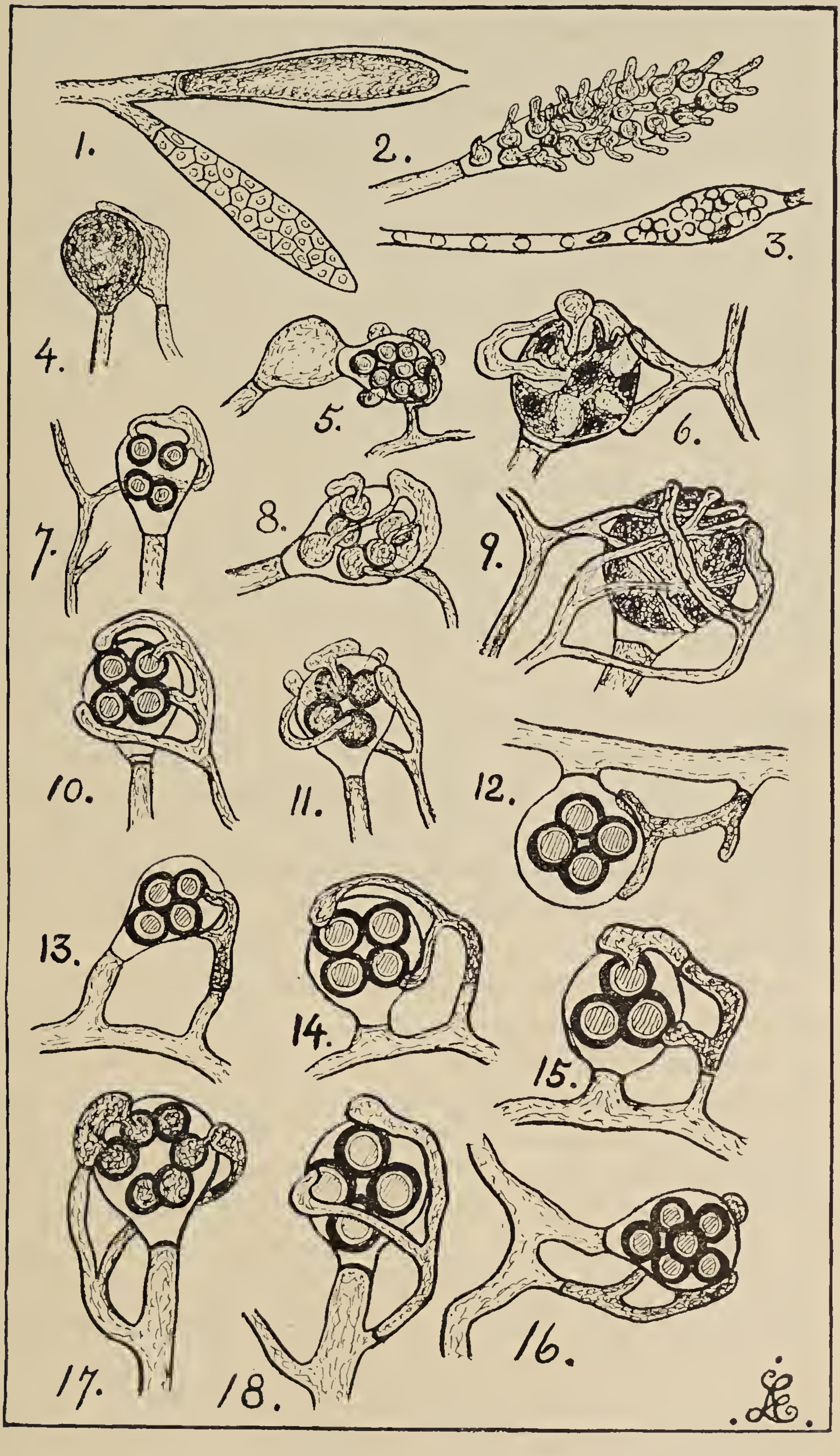
COMPARISON OF THE SPECIES.

From the general appearance of this species in the cultures and the facility with which it produces gemmæ, it showed a very close resemblance to the species described in the previous paper. The size and shape of the gemmæ and the methods of germination of the resting sporocyst type are identical in two cases. The general life-history, with the exception of the formation of oocysts and antherocysts is also identical.

The resemblance is further carried out by the occurrence of certain identical variations of the normal sporocyst, such as the *Achlya*-type of branching of the sporocyst, the *Aplanes*-type of sporocyst with the spores germinating *in situ*, the formation of Dictyosporocysts, and, lastly, the formation of multiple sporocysts, or chains of gemmæ.

The chief points of difference are the abundant formation of oocysts and antherocysts, and also parthenogenetic oocysts in the present species, and the comparative rarity of the occurrence of the multiple sporocysts or chain-gemmæ which were produced in great abundance in the last species.

The following characters are common to the present "Species I." and that referred to as "a species of *Saprolegnia*" in the previous paper:—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1. General appearance of the mycelium and dimensions of the hyphæ.
2. Size and shape of the normal sporocysts with diplanetic zoospores.
3. Formation and germination of the gemmæ.
4. Formation of multiple sporocysts (chain gemmæ).
5. Occurrence of *Achlya*-type of branching of sporocysts.
6. Occurrence of *Aplanes*-type of sporocyst.
7. Occurrence of Dictyosporocysts.

From the consideration of the points in common between these two species, it seems evident that they are identical.

It now remains to establish the species which will include all the characters shown by these two investigations.

DETERMINATION OF THE SPECIES.

In the case of the species in the previous paper, the exact species could not be determined, owing to the entire absence of the formation of sexual organs of reproduction, but from the frequent occurrence of the sporocyst it appeared to resemble *S. torulosa*.[1]

With the present species (Species I.), however, the case is quite different, as there is a plentiful formation of oocysts and antherocysts.

From the characters in general shown in the life-history of this species, and from the dimensions and appearance of the oospores and oocysts, and the varied arrangements of the antherocyst, and especially the formation, although rare in this case, of the multiple sporocysts, the present species corresponds very closely to that of *S. torulosa*.

The following full description of this species is given, taken from Rabenthorst—Kryptogamen Flora; *Saprolegnia torulosa*, de Bary, 1881 (3); Synon. *Saprolegnia* spec., Lindstedt, 1872 (13).

Mycelium consists of a fringe of hyphæ about 1 *cm.* composed of lax fairly thin branches (20μ thick). The hyphæ are at first cylindrical and of equal thickness throughout their length, bearing terminal, club-shaped sporocysts (zoospores diplanetic). After discharge a new sporocyst grows up within the wall of the old one, Later on several sporocysts are formed, one behind the other (multiple sporocysts), which arise as swellings—"Anschwellungen"—on the filaments with dense contents and separated from one another by transverse walls and delimited externally by slight constrictions (see figs. 11—14, Vol. IX., Pl. I.), so that when the older hyphæ thus become "torulated" the whole mycelium has the appearance of being *punctated.* The swellings (or gemmæ) are either club-shaped, pear-shaped, cylindrical, or sometimes irregularly shaped, and of very different size. On germination the gemmæ give rise to secondary gemmæ, secondary sporocysts or to oocysts. The sporocysts are of two kinds. The first kind resemble those of other species of *Saprolegnia*, as already described. The second kind occur later and are formed in a row one behind the other, or variously arranged according to the arrangement of the "swellings (chain gemmæ) from which they are formed.

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[1] See note after genus *Leptomitus*, N.P., Vol. IX., p. 308.

The terminal sporocyst of such a row discharges by a terminal process, the other by a lateral opening (figs. 11 and 14, Pl. I., Vol. IX).

Oocysts are formed from the swellings on the hyphæ and in the older filaments often differ very much in shape and size, sometimes in a row one behind the other and, more rarely, completely isolated. The oocysts remain firmly attached to the mycelial filament until the oospores are mature; they have a smooth, coloured, clearly defined wall, not punctated, and contain many oospores.

Antherocyst usually absent, but when present arises either from the end of an adjacent branch of the same hypha (androgynous), or from a separate branch of the mycelium (diklinous).

Oospores, many in each oocyst, spherical or sometimes unevenly polygonal, smooth membrane, 14—22μ in diameter. Resting period, ten days; on germination give rise to a mycelium directly or to a sporocyst. Gemmæ of different shapes formed from the swellings on the "torulose" hyphæ; on germination they give rise to a germ-tube or a sporocyst.

The foregoing account agrees in all essential features with the present species, the only point of difference being the duration of the resting period of the oospores. In the case of the present species only one case of germination has been observed (p. 172, fig. 16). The numerous oospores produced in the cultures showed no tendency to germinate even at the end of a month.

With the exception of this slight difference, the species agree so very closely that there seems to be no doubt they are identical.

CONCLUSION.

The present species, did not show the great variety of methods of asexual reproduction shown in the last species, nevertheless the variations on the ordinary asexual method were sufficiently frequent to attract attention. A point of great interest in the present species is that now, when oocysts and antherocysts do occur, they both show a great variety of form. The oocysts were found to be of two kinds, the first form showing a sexual process preceding the formation of the oospores, the second form entirely parthenogenetic and producing the oospores in greater numbers, approximately twice as many as the first form. The antherocysts showed the greatest variability in this species. They were found to be formed in three distinct ways. The first form derived from a separate branch of the mycelium, *diklinous*; the second form derived from a branch of the same main hypha which bears the oocyst on a lateral branch, *androgynous*. The third form derived from a branch of the hypha actually bearing the oocyst, *hypogynous*.

Each of these three forms has been made a point of distinction for the determination of the species of the genus (see table of classification), but in this species all three forms occur in the same cultures; two forms at least were often observed in the same hanging drop.

PART II.

EXAMINATION OF THE SECOND SPECIES.

Species II. THE mycelium is composed of numerous fairly robust hyphæ, seldom branching, which radiate out from the medium on which the fungus is growing, forming a dense fringe, sometimes rising above the level of the water. The diameter of the hyphæ is between 30μ—40μ, which is about twice that of the Species I.

Asexual Organs of Reproduction. The first formed sporocysts are perfectly normal in appearance. They are elongated and cylindrical in form and borne terminally on the main hyphæ, and always slightly broader than the supporting hypha. They vary greatly in length, but all discharge motile zoospores in the usual manner.

The zoospores are diplanetic and show the usual resting period in the encysted condition, followed by the second swarm stage, which is of longer duration than the first. The second resting period results in direct germination.

When once the sporocyst has been discharged there remains the question of the formation of the new sporocyst. It is typical of the genus *Saprolegnia* for this to take place by a simple upgrowth (durchwachsend) of the hypha within the discharged sporocyst. This process being repeated several times, a series of cases, one within the other, is produced, giving the appearance known as "nested sporocysts."

This process, with various modifications, was certainly found to occur (p. 180, fig. 8), but at the same time a second and entirely different process was noticed.

It has been previously noted that the sporocysts were often of different lengths, and the method of formation of the new sporocyst seems to depend to some extent upon the length of the first formed sporocyst.

The length of the sporocyst on a vigorous mycelium is usually eight to ten times the diameter, and, in the case of very long forms, twelve times or more.

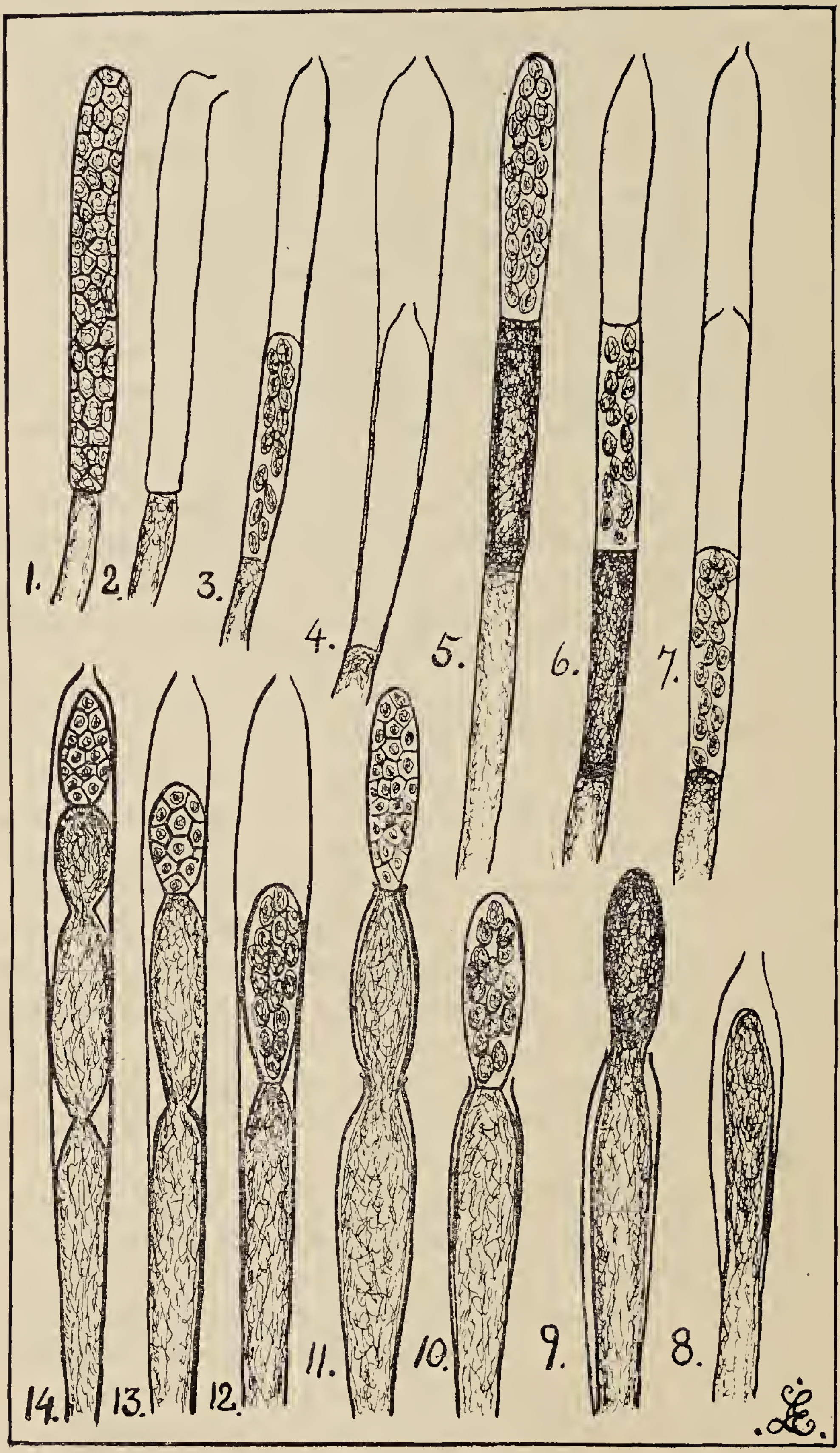
After observing the discharge of numerous sporocysts (p. 180, figs. 1 and 2), the cultures were watched in order to observe the upgrowth of the new sporocyst, and, on re-examining the next day, they showed for the most part the appearance of a new sporocyst formed immediately below the first one (p. 180, fig. 3); this same appearance could be produced by upgrowth within a long sporocyst terminating half-way (p. 180, fig. 4). Closer attention was paid to this point, and cases were found where the first formed sporocyst was ready to discharge the zoospores, and immediately below it a part of the hypha had been delimited, containing dense granular protoplasm and giving exactly the appearance of an early stage in sporocyst formation (p. 180, fig. 5).

After the discharge of the terminal sporocyst in such a case, the segment below was found soon to contain zoospores ready for discharge.

The discharge of this new sporocyst is terminal, and the zoospores have to traverse the empty cyst in front, before reaching the exterior proper (p. 180, fig. 6).

After the discharge of the second sporocyst, or during the formation of zoospores, a third sporocyst is formed, immediately below the second, in a similar manner (p. 180, figs. 6 and 7).

The third sporocyst proceeds to form and discharge its zoospores, which now have to traverse two empty cases in front of them before attaining freedom.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As they are not very active on discharge, the zoospores from the third sporocyst often do not reach the exterior, but encyst within one of the empty cases; examples were also noted where they had germinated in this position.

The greatest number of sporocysts found to have been formed in this way, and which have discharged motile zoospores, is three ; one case was noted where a fourth had been delimited, but no further development took place.

From the great number of cases observed, especially in the young and vigorous cultures, this method seems to be of fairly general occurrence in this species.

A second method of forming the new sporocyst was noted in cases where the first sporocyst was of the more usual club-shaped type instead of being, as in the first case, just described, of an elongated cylindrical form.

Here the hypha was found to grow up inside the empty case in the usual manner (p. 180, fig. 8), but when this had been completely filled, the growth of the hypha still continued, so that a protruding bud was formed ; this bud increased in size until it had the appearance of a somewhat smaller sporocyst born directly above the case of the first formed sporocyst (p. 180, fig. 9). In this position, zoospores were formed and discharged in the usual manner.

After the discharge of the second sporocyst, the process may be repeated so that a third sporocyst is formed on the top of the second; this, in turn, discharges its zoospores, leaving an empty terminal sporocyst.

The hypha, which now completely fills the first and second sporocyst, may continue growth and fill the third so that the filament has exactly the appearance of a resting multiple sporocyst (p. 184, fig. 6; p. 170, fig. 11), and this seems to be the general method; or the second sporocyst may proceed to form zoospores and discharge them through the empty terminal one, and the same process may occur with the first, so that in this way a series of three empty sporocysts would be left, each clearly limited by a marked constriction (p. 180, fig. 11).

In the figures, the walls of the sporocyst have been exaggerated for the sake of clearness, but in the actual cultures the hypha completely fills the sporocyst and cannot be distinguished from it when growth has ceased.

The discharging process has been marked to show the limitation of the sporocyst, but this is not seen in the actual cultures, as the sporocysts fit on to one another almost exactly, and it was only by watching the protruding end of the hypha that their formation in this manner was determined.

In the case of the hypha filling the third sporocyst, a chain of three resting sporocysts, or "chain gemmæ" is formed, having exactly the appearance of chain gemmæ formed in the ordinary way by simultaneous septation of several terminal segments (p. 184, figs. 6 and 7). On transferring the hyphæ showing this condition to fresh water they form sporocysts which are discharged in basipetal succession, as in the case of *S. torulosa*, but in this case the sporocysts have no separate openings, each discharging through the one in front.

At first this second method of new sporocyst formation seems in some ways to be exactly the reverse of the first method described, but, after the third sporocyst has been formed, the process is the same as that of the first, *i.e.*, basipetal sporocyst formation.

In old cultures the forms are very complicated and have various shapes. Several cases have been observed where, after a chain of three sporocysts has been formed, the hypha has continued growth as an ordinary filament (p. 184, fig. 4).

Filaments in the older cultures showing this condition present somewhat the appearance of the constricted hyphæ of the genus *Apodya* (*Leptomitus*), but no trace of constriction is found on the hyphæ of young mycelia.

No cases have been observed where more than three sporocysts were formed in this way. The older hyphæ show sometimes several septæ, but these are apparently formed simultaneously and represent a form of chain gemmæ (p. 184, fig. 7).

The third method of forming new sporocysts, and by far the more complicated, occurs in the case of the very elongated cylindrical form of first sporocyst.

After the discharge of such a sporocyst, a new one grows up inside it, but terminates at or below the level of half its length (p. 180, fig. 4). In this position formation and discharge of zoospores take place in the normal manner.

The empty case of the second sporocyst is now seen situated in the lower part of the first formed sporocyst.

Soon the hypha recommences growth and fills up the empty case and protrudes in the manner previously described till it forms a third sporocyst immediately above the second, both being contained within the original wall of the first. The third sporocyst is somewhat shorter in length than the second (p. 180, fig. 12).

After the formation and discharge of this third sporocyst, the hypha continues its growth, filling the empty case and forming a fourth sporocyst in a similar manner to the third.

This process can continue till a chain of four sporocysts is formed, all contained within the original elongated cylindrical sporocyst. After discharge of the small terminal sporocyst, or in case of its failing to discharge, the chain of sporocysts has exactly the appearance of a series of chain gemmæ, and in this condition they can remain unchanged for some time (p. 184, fig. 1).

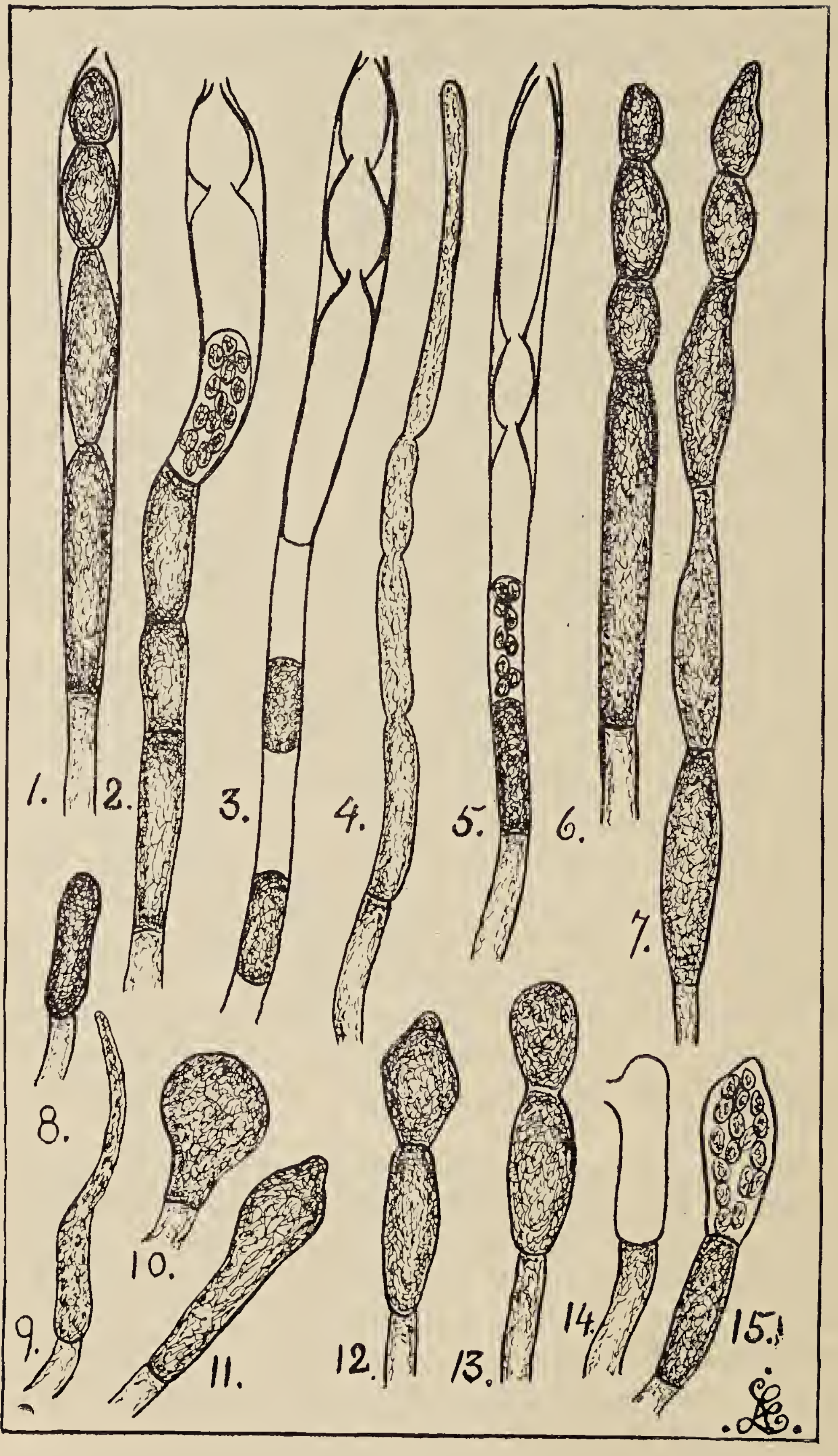
On transferring to fresh water, the discharge takes place in basipetal succession (p. 184, figs. 3 and 5), each sporocyst discharging through the empty one in front of it.

Old hyphæ frequently present a very complicated appearance, as the portion of the hypha below the original terminal sporocyst shows septation into a number of segments more or less constricted (p. 184, figs. 2 and 3).

The formation of new sporocysts in this species seems to be carried out with great persistence. Cases have been observed where, after the successive discharge of three sporocysts formed within the original terminal one, the hypha has again protruded into the empty case of the lowest of the chain, *i.e.*, the second in the process of formation, and produced a small sporocyst with zoospores, and, at the same time, a segment has been cut off immediately below it, having the appearance of a sporocyst at an early stage (p. 184, fig. 5). In this case there is the possibility of nine discharges taking place, if the last formed sporocyst succeeds in producing zoospores, but the case figured was never seen to discharge, so that not more than seven actual discharges have occurred.

After the discharge of a chain of sporocysts the old hyphæ often present the appearance of repeated segmentation for some distance below the terminal sporocyst. Alternate segments of this part of the hypha are seen to be densely filled with granular protoplasm, while the other parts appear quite empty. These segments have exactly the appearance of "resting sporocysts," and in this way may be considered as intercallary gemmæ. Their germination has not been observed (p. 184, fig. 3).

The Presence of Gemmæ. Gemmæ of various shapes were observed at all stages of the cultures after a few days' growth.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They may either be borne singly and terminally (p. 184, figs .8, 10 and 11), or they may show the presence of septæ (p. 184, figs. 6, 12 and 13).

In some cases, on the older hyphæ, a series of several septated segments is found forming a chain gemma (p. 184, figs. 6 and 7).

The germination may be vegetative (p. 184, fig. 9), but usually results in sporocyst (p. 184, figs. 14 and 15), or oocyst formation, as the case may be.

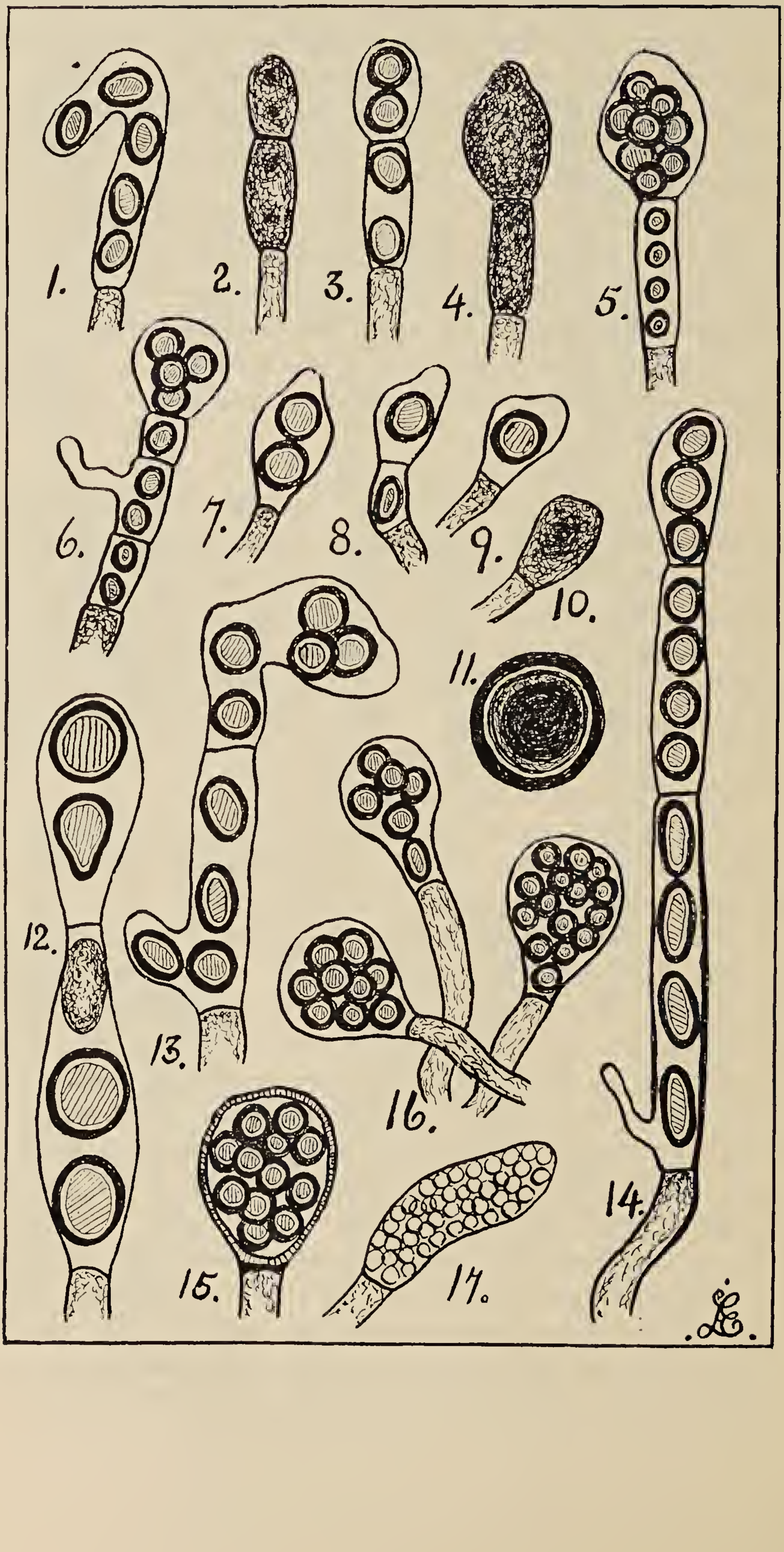
Mention may be made here of the fairly frequent appearance of Dictyosporocysts of the true *Dictyuchus* type (p. 186, fig. 17). They are always derived from gemmæ and in shape they are broad and short. The empty spore cases form a dense network within the sporocyst, the wall of which is very thin and is apparently directly penetrated by the zoospores on their escape from their encysted condition.

Sexual Organs of Reproduction. At a fairly early stage in the life history of this species, after about a week's growth, and before any signs of ordinary oocyst formation were observed, many cases were found of the formation of bodies which appeared to be oospores contained in organs exactly resembling sporocysts, that is to say they had the appearance of the ordinary sporocyst which had formed oospores instead of zoospores (p. 186, fig. 1). Several cases showing this condition were observed on a single culture, and were frequently met with from time to time on various cultures.

This type of oocyst, or transformed sporocyst, was often so narrow that the oospores were egg-shaped instead of spherical; the size also is found to vary to a great extent (20μ—30μ).

The cylindrical type of oocyst was often observed to result from the development of a multiple gemma. The contents of such a gemma is seen to divide into several distinct masses, usually four, but often only two (p. 186, fig. 7), and more rarely eight or an intermediate number (p. 186, figs. 2—4). Each of these masses later becomes clearly defined, with a distinct outer smooth membrane or exospore, which is fairly thick and of brown colour (p. 186, fig. 3). Often the terminal division is more spherical and contains a greater number of ova (p. 186, figs. 5 and 6).

One case was noticed showing great difference in size of the ova; a septated gemma developed into a terminal spherical oocyst and a cylindrical one below it (p. 186, figs. 4 and 5). The spherical oocyst contained eight oospores, average 24μ diameter, while the cylindrical part contained four diminutive oospores 18μ diameter.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Sometimes a series of cylindrical oospores is formed, derived from the development of a chain gemma. In this case almost invariably one of the segments shows the presence of a protuberance or germ tube (p. 186, figs. 6, 13 and 14).

Occasionally one of the masses in such an oocyst is seen to remain granular in appearance, with a delicate membrane, while all the others have formed the usual thick exposures (p. 186, fig. 12). No further development of these bodies has been noted, and no case of germination of the oospores kept for two months in various cultures has yet been observed.

Frequently in the cultures very small oocysts were found, only containing one oospore; these are derived from specially small gemma-like bodies (p. 186, figs. 9 and 10). Sometimes these small oocysts are multiple, and each contains one oospore (p. 186, fig. 8).

The Typical Oocysts. Besides the somewhat abnormal cases just described, oocysts of the ordinary type were found in great abundance. Their occurrence is first noted after about nine days, and on some of the older cultures, after fourteen days' growth, they were produced in such abundance that the whole mycelium had the appearance of being densely covered with minute spots.

The oocysts are borne singly and terminally on lateral branches of the main hyphæ, or on short hyphæ arising from the base of the mycelium; they are spherical or pear-shaped, and remain firmly attached to the hypha which bears them.

The wall of the oocyst is fairly thin and not deeply coloured, usually quite free from spots, but some show the presence of a few ill-defined patches on the wall. No case has been observed where the spots are clearly defined or occur as distinct coloured patches.

The Oospores. The number of oospores produced varies to some extent. The usual number appears to be eight in the typical form of oocyst, but frequently as many as twelve are found, and sometimes only six. Reference has already been made to the occurrence of single oospores.

The size of the oospores also varies greatly, 20μ—30μ, but the average for typical oocysts is 22μ.

In the cylindrical form of oocyst, the diameter of the larger oospores is 27μ, average size. The presence of the specially small oospores may be considered abnormal and of only rare occurrence.

The oospores are usually spherical, but occasionally oval in the narrow oocysts. They have a clearly defined, perfectly smooth, brown coloured outer membrane or exospore, and a thinner colourless endospore. The contents are composed of granular protoplasm, containing a deeply coloured concentric globule of fat (p. 186, fig. 11). Germination has not been observed.

The foregoing is the full account of the various methods of reproduction found in this species while following its life history by means of various cultures in the manner already described for Species I. Before proceeding to the determination of the species and genus, the following brief summary of the chief characters is given.

SUMMARY OF THE LIFE HISTORY OF THE SPECIES II.

Mycelium composed of fairly stout unicellular hyphæ, average 30μ diameter, bearing terminal cylindrical sporocysts, zoospores are discharged through terminal opening and are diplanetic. New sporocyst frequently formed from a segment of the hypha cut off immediately below discharged sporocyst: Zoospores from second sporocyst discharged through empty case of first. Sporocyst formation may continue by retrogressive segmentation of the hypha. Upgrowth (durchwachsend) of the hypha also occurs and frequently continues beyond the limits of the sporocyst wall, forming a superposed sporocyst. Multiple sporocysts are often found and may form chain gemmæ. Ordinary gemmæ of various shapes also occur and on germination give rise to sporocysts or oocysts. The oocysts are spherical, pear- or barrel-shaped, and are borne singly on lateral branches to which they remain firmly attached; they occur in large numbers and usually contain many ova (six to twelve). Special small oocysts are found containing only one oospore. The first formed oocysts are often cylindrical in shape and resemble sporocysts containing ova. No trace of the presence of an antherocyst is found.

GENERAL CLASSIFICATION OF THE FAMILY.

In the last paper only a very brief table of genera was given, based entirely on the variation in forms of asexual reproduction. The full table of classification of the family is given below, taken from Rabenhorst (17), after de Bary (3, 4).

TABLE I.

CLASSIFICATION OF THE SAPROLEGNIACEÆ

(From Rabenhorst-Cryptogamen Flora, Abt. IV., p. 326),

SUB-FAMILY SAPROLEGNIACEÆ.

Mycelium composed of cylindrical hyphæ of uniform diameter not constricted into segments.

I. Spores after discharge swarm and germinate outside the sporocyst.

(1). All spores discharge from the sporocyst through the same opening.

- a. Zoospores discharged motile and immediately disperse by active swarming.
- aa. Monoplanetic.
  - α. Sporocysts egg-shaped; after discharge new sporocysts arise as a lateral branch. *Pythiopsis.*
- bb. Diplanetic.
  - Elongated sporocysts; after discharge new sporocyst grows up inside the wall of the old one.
  - α. Sporocysts club-shaped; containing many rows of spores. Oocysts contain many oospheres. *Saprolegnia.*
  - β. Sporocysts tubular; containing a single row of spores. Oocysts contain a single oosphere. *Leptolegnia.*
- b. Zoospores non-motile on discharge; collecting at mouth of sporocyst to form a hollow sphere before encystment.
- aa. Sporocysts club-shaped; containing many rows of spores. Oocyst contain many oospheres. Thick membrane. *Achlya.*
- bb. Sporocysts tubular; containing one row of spores (amœboid). Oocysts contain a single oosphere. Membrane very thin. *Aphanomyces.*

(2). Each spore encysts within sporocyst and is discharged through a separate opening, and immediately swarms away; a polygonal network of cell-walls remains behind in the sporocyst. *Dictyuchus.*

II. Spores not discharged from sporocyst; no swarming occurs, but spores germinate within the sporocyst. *Aplanes.*

SUB-FAMILY APODYEÆ (LEPTOMITACEÆ).

Mycelium composed of hyphæ constricted at approximately equal distances into segments.

1. Zoospores formed within the sporocysts and are all discharged through the same opening.
   - a. Zoospores immediately disperse by active swarming. *Apodya.*
   - b. Zoospores show feeble swarming and encyst near the sporocyst. *Apodachlya.*

(2). Zoospores formed outside the sporocyst. The contents of sporocyst is discharged as a bladder-like mass, from which the zoospores are formed and discharged later. *Rhypidium.*

From the consideration of the sum total of the character of Species II., given in the Summary, it seems to belong, undoubtedly, to the genus *Saprolegnia*; but on two points, at any rate, it approaches the genus *Apodya.*

The following general description of these two genera is given:—

GENUS *Saprolegnia*, NEES. *v.* ESENBECK. 1823.

Mycelium composed of stout radiating hyphæ, bluntly rounded at the apex. Main hyphæ unbranched or with monopodial branching at time of sporocyst formation. Sporocysts are formed terminally on the main hypha or its branches; they are cylindrical or club-shaped and contain many rows of zoospores; discharge takes place by means of a terminal opening of which the orifice is often drawn out into a short tubular process. After discharge, upgrowth (durchwachsend) of the hypha takes place within the sporocyst; this process is usually repeated several times, giving the appearance known as "nested sporocysts."

Zoospores, unicellular, discharged in the motile state and immediately disperse by active swarming; they are diplanetic. The first form, egg-shaped, with the apex drawn out into a point bearing out two terminal cilia, comes to rest after a few minutes becomes spherical and secretes a membrane. After a short resting period, the contents creep out and forms a new zoospore. This second form of zoospore is kidney-shaped, with two lateral unequal cilia, swarms for a longer period and later germinates to form a mycelium.

Oocysts, usually terminal, but sometimes intercalary, or variously arranged; chiefly borne in clusters, which may occur terminally on the main hypha, but more usually on short lateral branches arising from it. The oocysts are spherical, pear- or barrel-shaped, smooth or spiny, usually spotted, and have a moderately thin membraue. In most species the oocyst contains many oospores, but in some species the oocyst regularly contains only one oospore; this condition may also occur as a variation in species which usually have many ova.

Antherocysts, egg- or curved club-shaped structures of small size, borne terminally on an antheridial filament (Nebenästen), which may arise either from the main hypha bearing the oocyst (androgynous), or from separate branch of the main hypha (diklinous). In some cases it is cylindrical and arises from the same branch which bears the oocyst (hypogynous).

When the antherocysts are not present, the oospores nearly always mature parthenogenically. The oospores are spherical. smooth, with a thick, coloured, glistening exospore and a thinner endospore, and brown or yellow contents with a concentric or excentric globule of fat.

Gemmæ of very different sizes and shapes often occur,

GENUS *Apodya*, CORNU, 1872.

Mycelium composed of hyphæ, monopodially branched in the same manner as *Saprolegnia*, but divided into cylindrical segments by constrictions at approximately equal intervals.

The segments thus formed are not separated by definite transverse walls, but each segment contains one or more disc-shaped cellulin bodies, usually situated in the neighbourhood of the constriction.

New segments are formed by apical growth of the hypha. Multiplication of the segments by subsequent constriction of an already completed segment does not occur. Lateral branches arise always from the upper part of a segment just below the constriction and have a constriction at their base.

Sporocysts are terminal and borne singly, or one behind the other, by basipetal development of the existing segments, which then become separated by plugs of cellulin in the constricted area.

Each sporocyst is formed from one segment which becomes more or less swollen. The discharge takes place by means of a terminal process, but when a row of sporocysts occurs, these below the terminal sporocyst discharge by means of lateral processes. New sporocysts can arise by upgrowth of hypha, as in *Saprolegnia*, by lateral branching of the hypha, as in *Achlya*, or by basipetal transformation of successive segments.

Zoospores are unicellular, egg-shaped, with two equal terminal cilia, and are discharged motile and immediately disperse by active swarming, possibly diplanetic.

Sexual organs and oospores unknown.

The genus *Apodya* comprises one single species, *A. Lactea* separated by Cornu, 1872, from the genus *Leptomitus*, where it had been placed by Argardh, 1824.

The remaining twenty-nine species of the genus *Leptomitus* mentioned by Kützung in his " Species Algarum " do not belong to the Saprolegniaceæ at all.

Below is given a list of the synonyms of this species:—

Apodya lactea. (Argardh, 1824), Cornu, 1872.
Synon. *Conferva lactea.* Roth bei Dillwy, 1809, Brit. Conferv. Tab. 79.
Leptomitus lacteus. Argardh, 1824, spec. Alg.
,, ,, ,, bei Kützung, 1843, Phycol. Germ.
Saprolegnia Liberiiæ (Argardh) Kützung 1849, Spec. Alg.
,, *lactea.* Argardh bei A. Braun, 1851, Verjüngung.
,, ,, (Argardh) Pringsheim, 1860, Jahrb. wiss. Bot. II.
,, *dichotoma.* Suhr. in Breutel Flor. Germ. exs. 206.
,, *corcagiensis.* Hartog, 1887, Q.J.M.S., XXVII.

From the foregoing account of the genus *Apodya*, it will be seen that on two points Species II. is in close agreement.

In the first place, on account of the method of forming sporocysts by basipetal transformation of successive segments of the hypha, and, in the second place, by the occurrence of the ordinary *Saprolegnia* method of upgrowth of the hypha through the sporocyst.

On all other points it bears no resemblance to the genus *Apodya*; and even in the point which bears the closest resemblance, namely, the formation of sporocysts one behind the other from successive segments, it will be noticed that each segment in the genus *Apodya* is said to discharge by means of a separate process, whereas in Species II, when this arrangement of sporocyst occurred, each sporocyst discharged through the one above it. Moreover, from the great number of oocysts produced and their general structure, there seems to be no doubt that this Species II. belongs to the genus *Saprolegnia*, as oocysts are not known to occur in the genus *Apodya*.

The genus *Saprolegnia* is very much more complicated, as it comprises many species; these may be conveniently divided into three groups, according to the type of oocyst. A table of classifiication is given, before commencing the determination of the species.

Genus *Saprolegnia*.

Classification of the Species, [de Bary (3) and (4)].

Ferax-Group. Oocyst has smooth wall, contains many oospores and remains firmly attached to hypha until spores are mature.

Monolifera-Group. Oocyst has smooth wall, contains many oospores, but separates from the hypha at an early stage before oospores are mature.

Asterophora-Group. Ooocyst star-shaped, with spiny projections and only contains a single oospore.

Table of Species.

TABLE II.

I. Oocyst smooth, containing many oospores.

  1. Oocyst remains firmly attached to mycelium till oospores are mature. New sporocyst grows up within wall of old one. Ferax Group.

    A. Antherocyst nearly always present.

    aa. Antherocyst arises from same branch, which bears the oocyst (hypogynous), never formed from an adjacent filament. *S. hypogyna* (*1*).

bb. Antherocyst formed from a separate filament.

α. Antheridial filament arises as a separate branch from the main hypha (diklinous).

αα. Oospore concentric, zoospores all of one kind. *S. dioica* (*2*).

ββ. Oospores excentric, zoospores of two kinds. *S. anisospora* (*3*).

β. Antheridial filament arises from same main hypha which bears the oocysts (androgynous).

αα. Antherocysts always present. *S. monoica* (*4*).

ββ. Antherocysts only present in 50% cases. *S. mixta* (*5*).

B. Antherocyst nearly always absent.

aa. Oocysts borne singly. Main hyphæ robust and of even thickness. Antherocyst never present. *S. Thureti* (*6*).

bb. Oocysts often in rows, main hyphæ lax, and later become divided into segments forming gemmæ, oocysts or secondary sporocysts. Antherocysts sometimes present.

S. torulosa (*7*).

(2). Oocysts contain many oospores and become detached from the hpyha before the oospores are mature, or only remain very slightly attached. New sporocysts arise by upgrowth within old wall or by cymose branching of the hyphæ. MONILIFERA GROUP. *S. Monilifera* (*8.*)

II. Oocyst spiny, star-shaped, only contains one oospore. New sporocyst arises by upgrowth of hypha within the old wall.

ASTEROPHORA GROUP. *S. Asterophora* (*9*).

THE DETERMINATION OF THE SPECIES.

Owing to the fact that the oocysts are smooth, contain many ova, and remain firmly attached to the hyphæ, this species evidently falls into the *ferax*-group.

Following the classification just given of this group, it is seen to come into the second division, characterised by the absence of the antherocyst. This limits the species to *S. Thureti* or *S. torulosa*.

As mentioned in the first part of this paper, the two species under investigation showed sufficient differences in the cultures to be separated as Species I. and Species II. respectively. This separation was carried out and each investigated separately, with the result that Species I. was determined as *S. torulosa*. There now remains for the determination of Species II, only *S. Thureti*, if it is to be really distinct from Species I.

On all points of general appearance of the hypæ in the cultures it certainly does appear to be a distinct speeies.

In his summary of the *ferax*-group, de Bary (5) shows that the so-called *S. ferax* can really be resolved into at least three distinct, yet closely related species, viz., *S. monoica*, *S. Thureti* and *S. torulosa*. A fourth species may also be included, *S. mixta*, which may be only a variety of *S. monoica*.

The absence of the antherocyst, although complete in this case, must not be taken as conclusive, as the presence of the organ is known to be variable in the group. On many points, the present species resembles another species in this group—*S. dioica*, at least in so far as can be made out from text descriptions.

A short description of each of these species of the *ferax*-group with the exception of *S. torulosa* is given below, so that comparison can be made of the points in common.

I. *S. Dioica*, de Bary (5, 17).

Mycelium, slender lax hyphæ 20-40μ thick, bearing long cylindrical or club-shaped sporocysts, very slightly wider than the hyphæ and often very long and slender, 80-400μ.

After the discharge, new sporocysts grow up repeatedly within the old wall, each one successively shorter than the precedent, so that the nesting of the successively formed sporocysts after their discharge is very clearly shown.

Oosysts are terminal or intercalary, either borne singly or in a row one behind the other on the main hyphæ. They are spherical, pear- or barrel-shaped, and vary very much in size. The membrane is smooth, usually of a yellowish colour, either with a few small spots or not spotted at all.

The oocysts contain many oospores, up to twenty, in the same oocyst. The oospores are spherical, smooth, concentric, 25-30μ diameter, germination unknown.

Antherocysts are always present, usually very numerous, and are borne terminally or in a row one behind the other on the antheridial filaments which arise from a separate main hypha (diklinous).

The S. *dioica*, de Bary (1883), just described is a clearly defined species and must not be confused with the S. "*dioca*" of other authors, of which the following are instances:—

S. *dioica*, Pringsheim, 1860, Jahr. wiss. Bot. II, Tag. XXII., is shown to be S. *Thureti* and occurred mixed with *Rozella septigena* in the same culture. All species described as S. *dioica* by earlier authors have also been found to belong to S. *Thureti*, as none of them showed the diklinous origin of the antherocyst, which is the charateristic of this species.

S. *dioica*, *var racemosa*, de la Rue, 1869. Bull. soc. imp. Nat. Moscow, XLII. This is shown to be really S. *Thureti*, from which it is only distinguished by the abnormal branching of the main hypha.

S. *dioica*, Schröter, Ber. schles. Ges. vaterl. Cult. This has also been shown by later authors to be none other than S. *Thureti*.

II. S. *Monoica*, de Bary (1881).

id. Pringheim, 1858, Jahrb. f. wiss. Bot. I.

id. Reineke, 1869, Arch. Mikr. Anal. V.

Sinon: *Diplanes saprolegnoides*. Left. geb. 1870, Jahrb. f. wiss. Bot. VII.

Achlya intermedia. Bail, 1860, Naturf. Ver. Königsberg.

Saprolegnia spiralis. Cornu, 1872. Ann. des. Sci. Nat. Bot. Ser. V, tome XV. (Not a very complete description of this species is given, but it seems to be very close to S. *monoica*, from which it differs chiefly in having the hypha which bears the oocysts spirally curved and in the number and colour of the oospores).

Mycelium, stout hyphæ, as much as 75μ thick, standing up out of the water, bearing either terminal or lateral sporocysts, which are cylindrical or club-shaped and vary much in size; several sporocysts are formed within the original case, forming "nested sporocysts.

Oocysts are spherical with a few fairly large spots on the smooth coloured wall. They contain many oospores. The oocysts are frequently borne terminally on short lateral branches, which spring in clusters from the main hypha. In some cases a more or less distinct "Oogoniaphore" may be formed terminating in a sterile hypha, a sporocyst, or an oocyst. Ooospores, spherical, concentric, 16—22μ, smooth, occasionally borne singly in an oocyst, but usually five or ten, and rarely as many as thirty in the same group. Resting period, 68 to 145 days.

Antherocysts are always present and arise as lateral branches near the oocysts from the same main hyphæ (androgynous).

IIa. *S. monoica* var. *montana*, de Bary (1888).

Distinguished from the type species by a few minor differences only. The hyphæ are much more delicate, having a lax appearance The hypha bearing the oocysts is often very very elongated and irregular in form. The oocysts have thicker membranes, quite smooth, with entire absence of spots.

III. *S. Mixta*, de Bary (1888).

Mycelium, delicate lax hyphæ, sporocysts resembling those of the species.

Oocysts are distinguished by having very large prominent spots on the membrane. Oospores numerous and resemble those of the other species.

Antherocysts (usually diklinous) present in 50% of the cases.

IV. *S. Thureti*, de Bary (1881).

Synon. *S. ferax* (Gruith) Thuret, 1850.

The *S. ferax* of other authors are quite distinct from this species, and when the name "ferax" is retained it must be indicated as above, not as *S. ferax* (Gruith), Kützing, etc. To avoid all confusion, it is better to adopt the name given by de Bary, and completely banish the name ferax.

Mycelium consists of stout, robust hyphæ, often standing up above the water-level, in some cases as much as 75μ thick, yet always more lax at times of oospore formation.

Sporocysts are borne terminally on the main and lateral hyphæ; they are club-shaped or cylindrical, vary very much in thickness and length, but are always rather thicker than the supporting hypha. After the discharge, upgrowth of the hypha occurs repeatedly, forming nested sporocysts.

Oocysts are borne singly on the main or lateral branches; they are spherical or pear-shaped, with many fairly large spots on the smooth coloured wall. The oocysts are sometimes cylindrical and may be formed within a discharged sporocyst; they usually contain many oospores, but occasionally specially small oocysts are formed which only contain one oospore.

Oospores, spherical, smooth, concentric, 20—27μ diameter. Resting period, 45—92 days. Germination by means of germ tube or sporocyst formation.

Antherocysts and antheridial filaments entirely absent.

A table is given below showing a comparison of the variations which exist between the various species composing the *Ferax* group (with the exception of *S. hypogyna* and *S. anisospora*, which have special characteristics) and the Species II., under investigation.

GENERAL REMARKS ON THE AFFINITIES OF SPECIES II.

Taking into consideration the general characters shown in the life-history of Species II., it will be seen that a very close relationship exists between it, *S. dioica*, *S. Thureti*, and *S. torulosa*.

Points of resemblance between Species II. and the genus *Apodya* have already been referred to and seem to be in this case more of the nature of a chance variation than having any specific value.

The points of resemblance between Species II. and *S. torulosa* are the following:—

1. Occurrence of oocysts in rows and singly.
2. Wall of oocyst not spotted.
3. Special small oocysts with one oospore.
4. Occurrence of gemmæ.
5. Older hyphæ show septation into segments.

TABLE III.

The *Ferax* Group.

	S. dioica.	*S. monoica.*	*S. mixta.*	*S. Thureti.*	*S. torulosa.*	*S. Species II.*
Hyphæ	lax, 20—70μ.	stout, 75μ.	lax, 90μ.	stout, 40—75μ.	lax, 15—20μ.	stout, 20—40μ.
Oocysts	single or in rows, spherical, pear- or barrel-shaped, wall smooth, with small spots or not spotted at all.	in clusters, spherical or pear-shaped, wall smooth, with a few large spots.	singly or clusters, spherical or pear-shaped, wall has large prominent spots.	singly, spherical, pear-shaped or cylindrical, wall smooth, with many large spots.	singly or in rows, spherical, pear- or barrel-shaped, wall smooth, not spotted at all.	singly and in rows, spherical, pear-shaped and cylindrical wall smooth, not spotted.
Oospores	up to 20 in each oocyst.	5—10 to 30 in each oocyst.	5—10 in each oocyst.	6, 12, 20 and sometimes only 1 in special small oocyst.	6, 12, 20 and sometimes only 1 in special small oocyst.	6, 12 in each oocyst and often only 1 in a very small oocyst.
,, diameter	25—30μ.	16—22μ.	16—22μ.	20—27μ.	14—22μ.	22—27μ.
Resting period ...	unknown.	63—145 days.	—	45—92 days.	10 days (?).	not determined.
Antherocyst ...	always present diklinous.	always present androgynous.	present in 50% cases, usually diklinous.	never present.	seldom present.	never present.

The following points of resemblance exist between Species II. and *S. dioica* :—

1. Occurrence of oocysts singly and in rows.
2. Wall of oocyst sometimes not spotted.
3. Diameter of oospore.
4. Undetermined resting period.

The resemblance between Species II. and *S. Thureti* is very close, the following points are common to the two species :—

1. Stout hyphæ$=40\mu$.
2. Shape of oocysts (ordinary).
3. Occurrence of cylindrical oocyst.
4. Occurrence of special small oocysts with one oospore.
5. Number and diameter of oospores.
6. Resting period more than forty days.
7. Entire absence of antherocysts.

In any case, the resemblance between *S. dioica* and *S. Thureti* is known to be very close, as will be seen from the note following the description of the former species. Many earlier workers had described species under this name which were later found only to be a form of *S. Thureti.* The character on which *S. dioica* is absolutely determined is that of the unfailing presence of the diklinous antheridial filament. From the fact that Species II. never showed the least trace of an antheridial filament, the possibility of classing it as *S. dioica* must be rejected.

The reasons have already been discussed for its not being classed as *S. torulosa.* There now remains only *S. Thureti*, to which the resemblance is so very close there seems little doubt that it may be classed as this species.

The only points of difference between Species II. and *S. Thureti* are :—

1. The absence of spots on the oocyst wall.
2. The occasional formation of oocysts in rows.
3. The undetermined resting period.
4. Various modifications of the method of forming new sporocysts.

Of these differences, the only point which is of any real value in determining the species is the absence of spots on the oocyst wall. This point in itself may easily be variable within the limits of this species; as in the closely related species *S. dioica*, the membrane is found to be either spotted or quite plain.

The occurrence of oocysts in rows may be looked upon as a consequence of the germination of the various rows of chain gemmæ from which they were invariably formed.

As regards the duration of the resting period, much stress cannot be put on this point, which shows such great variation in all the species and must necessarily depend to a great extent upon external conditions.

The last point of difference must be regarded as a special variation rather than as showing any specific distinction.

CONCLUSION.

Upon the following general characters shown by Species II., I then base my decision for determining this species as that of *S. Thureti*, de Bary, 1881. (Synon. *S. ferax* (Gruith) Thuret, 1850).

1. Stout hyphæ (30—40μ) on the young mycelia becoming more lax during oocyst formation.
2. Elongated cylindrical sporocysts of different lengths, often only slightly wider than the hyphæ.
3. The repeated upgrowth of the hypha within the discharged sporocyst. (This process being capable of many variations).
4. The presence of cylindrical oocysts with the oospores in a row.
5. Shape and size of the ordinary oocysts.
6. The presence of specially small oocysts containing a single oospore.
7. The numbers of the oospores, 6—12.
8. The diameter of the oospores, 22—27μ.
9. The entire absence of antheridial filaments and antherocysts.

SUMMARY.

As the result of the investigation of Species I., the following facts have been established:—

1. It is identical with the species described previously (NEW PHYT., Vol. IX.), but not named specifically.
2. Owing to the formation of sexual organs of reproduction, as well as the various asexual methods, the species has been established as that of *S. torulosa*, de Bary.

3. The sexual organs, when found to be present, present almost as great a variety of form as has already been mentioned as occurring in the case of asexual methods of reproduction.

As the result of the investigation of Species II., the following facts have been established:—

1. It is determined as *S. Thureti* de Bary, from a consideration of all general characteristics.
2. It shows two peculiar variations in the method of formation of new sporocysts:—
    (A). Formation of new sporocyst by basipetal segmentation of the hypha, described for the first time as occurring in the genus *Saprolegnia.*
    (B). Various modifications of the method of new sporocyst formation by repeated upgrowth of the hypha.
3. It shows septation of the older hyphæ into segments. a habit formerly described as a characteristic of *S. torulosa.*
4. The presence of gemmæ, not previously noted for this species.
5. The occurrence of oocysts in a row, not previously noted for this species, but described as found in *S. dioica* and *S. torulosa.*
6. The absence of spots on the oocyst wall, regarded as a variation, not previously mentioned as occurring in this species.

I should like to take this opportunity of correcting some errors in my previous paper (New Phyt., Vol. IX., p. 305).

In the Analysis of Genera, p. 308, insert after § *Leptolegnia: and the sporocysts contain a single row of zoospores.*

Page 315 § (5). For *Leptomitus*-type read *Leptolegnia*-type, and for genus *Leptomitus* read genus *Leptolegnia.*

Page 318, Summary. For *Leptomitus* read *Leptolegnia.*

Finally, I should like to take this opportunity of expressing my very sincere thanks to Monsieur L. Mangin, Membre de l'Institut,

Professeur au Muséum d'Histoire Naturelle, for kindly allowing me to publish this account in an English Botanical journal, and, at the same time, for the kind interest he has shown in this work and for the provision of all material and apparatus necessary for this investigation.

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NOTE ON THE VASCULAR CONNECTIONS OF THE SPOROCARP IN *MARSILIA POLYCARPA*. HOOK & GREV.

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[PLATE III].

THE sporocarp of *Marsilia* has been regarded as a ventral lobe of the leaf by Van Tieghem (6), but Dr. M. A. Chrysler (3) figures a section through the petiole of *Marsilia quadrifolia* Linn. at the point of attachment of the stalk of the sporocarp, showing that the origin of its vascular supply is from one edge of the curved leaf-trace. Goebel (4) has studied developmentally and described how in another species, *Marsilia polycarpa*, several sporocarps arise in acropetal succession on one side of the petiole. As the vascular connections in this species have not yet been described or figured, it was thought that it would be worth while to make observations upon it, so Professor Bower handed over to me material which he had received some years ago from Jamaica.

In *Marsilia polycarpa* the petiole bears a varying number of sporocarps, usually from four to nine, arising acropetally on one side of the petiole, while the distal lamina is, as in *Marsilia quadrifolia* divided into four lobes.

In the rhizome of *M. polycarpa*, a typical solenostelic condition is found. It has an outer cortex with air-canals, as in the petiole, separated from the inner cortex by a band of sclerenchyma. The vascular system consists of a continuous ring of xylem, in most parts two cells deep, surrounded by phloem and pericycle both on the exterior and interior, with a prominent external and internal endodermis. In the central part of the pith a small mass of sclerenchyma is present. At the insertion of the petiole the solenostele begins to elongate, the outer endodermis extending into the petiole base, followed by the xylem and inner endodermis which thus form a loop. Finally the xylem breaks off at one side, and the endodermis curves into the gap, which is soon completely closed by the joining up of the xylem.

The structure of the petiole corresponds to that shown by Campbell (2) for *M. quadrifolia*. The leaf-trace consists of a V-shaped xylem strand, surrounded by phloem and pericycle. The V is somewhat flattened, and at the apex the protoxylem elements are found, bordering on a canal probably formed by the disintegration of the earliest tracheids (Fig. 1).

As the point of attachment of the stalk of the sporocarp is approached, the vascular strand is found to become rather extended towards one side. One arm of the V stretches out (Fig. 2), and at this point the air-spaces disappear, and the band of sclerenchyma broadens and is practically continuous with the endodermis. The parenchyma of the pericycle now begins to intrude, and the vascular bundle of the sporocarp is nipped off from the lengthened arm of the xylem strand. The pericycle is followed by the endodermis and the small strand is thus separated from the main strand of the petiole by an intrusion of parenchyma (Fig. 3). After the bundle of the sporocarp has been nipped off, the arm of the V on that side remains elongated, and the vascular strand of the sporocarp next in succession comes off in exactly the same manner as the first sporocarp. The arm of the V elongates even more than in the first case, and the margin separates off to form the bundle of the stalk. This occurs in the succeeding sporocarps.

At the distal end of the leaf, four wedge-shaped leaflets are present. Sections were cut from about $\frac{1}{8}''$ below the insertion of the leaflets on the petiole, through the insertion of the leaflets and through the leaflets themselves. In the petiole itself the cross section is similar to that of the petiole below the attachment of the sporocarps. The vascular strand is marked off by a well-defined endodermis, and the single leaf-trace is V-shaped (Fig. 4). In the sections nearer the point of insertion of the leaflets, the petiole is found to have increased in diameter and the arms of the strand become somewhat flattened. The xylem shows signs of breaking up into three separate groups (Fig. 5), each group having a tendency to turn out at the two ends. By this time the whole section has assumed the shape of the three xylem-groups (Fig. 6), and the pericycle creeps in between the out-turned ends. Following the pericycle is the endodermis, and a group of xylem elements, surrounded by phloem and endodermis, occupies each of the three lobes of the petiole. These three lobes finally become separate (Fig. 7); but before separation, the single bundles of the lateral lobes have divided into two, while the bundle of the median lobe also begins to divide. As soon as the bundle of the median lobe has divided into two by splitting across (Fig. 8), a constriction appears above the split and gradually deepens until it divides the lobe into two elongated segments, the leaflets (Fig. 9). The bundles divide rapidly and in the leaflets many bundles are present.

In *Pteris semipinnata*, Linn. a species with pinnules on one side only of the pinna, it was found that the vascular strands of the pinnules came off from the margin of the strand of the pinna in the same manner as the vascular strand of the stalk of the sporocarp in *M. polycarpa.*

It is thus seen that the condition in *M. polycarpa* is exactly that in *M. quadrifolia.* In sections through the point of attachment of the sporocarp in both species, the vascular supply of the stalk is from the margin of the curved leaf-trace. The origin of the leaflets is also from the margin of the leaf-trace and this similarity in origin of the sporocarps and leaflets indicates structurally that the sporocarps are fertile lobes of the leaf in this as in other species of the genus. Further the comparison with *P. semipinnata* shows that the condition of *M. polycarpa* has its correlative in the leaves of a well-known Leptosporangiate fern.

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DESCRIPTION OF PLATE.

Figs. 1-3. Transverse sections of petiole. ×175.

Fig. 1. Transverse section taken a short distance below attachment of the lowest sporocarp of the leaf.

Fig. 2. Transverse section of the vascular strand just at point of attachment of the vascular supply to the sporocarp.

Fig. 3. Transverse section of the vascular strand after departure of the vascular supply to the sporocarp.

Figs. 4-9. Transverse sections of petiole and leaflets. ×26.

Figs. 4-6. Series of transverse sections of petiole below leaflets showing the marginal branching of the vascular supply.

Fig. 7. Transverse section showing the first two leaflets already detached from the rachis.

Fig. 9. Transverse section showing constriction of the rachis itself to form the last two pinnæ.

Fig. 9. Transverse section of four leaflets.

THE LIFE-HISTORY OF THE PLUM-RUST IN ENGLAND.

By F. T. Brooks, M.A.

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UNTIL recently it was not known whether an æcidial stage was present in the life-cycle of the Plum-Rust, *Puccinia Pruni*, Pers., but in 1904 Tranzschel,[1] working in Russia, shewed that *Æcidium punctatum* on *Anemone coronaria* was the alternate phase of this fungus. More recently still, Arthur[2] in the United States has confirmed the heterœcism of the Plum-Rust by proving experimentally that the æcidium on *Hepatica acutiloba*—a plant very closely allied to *Anemone coronaria*, is a stage in the life-cycle of this fungus.

Æcidium punctatum occurs on *Anemone coronaria* in England and the Rust on Plum leaves is becoming more common year by year in fruit-growing districts, but as far as I am aware no experiments have hitherto been performed to see whether this æcidium is a stage in the life-cycle of the Plum-Rust as it occurs in this country. It is important that this should be done because it is becoming more and more recognised that the life-histories of Rust-Fungi, especially the heterœcious species, should be worked out for each country separately.

Towards the end of April some material of *Æcidium punctatum* growing on *Anemone coronaria* in the neighbourhood of Cambridge was brought to me by Mr. Laidlaw, a student working in the Botany School, so it was thought desirable to ascertain if Plum-Rust could be induced by placing these æcidiospores on the leaves of a healthy Plum-tree. For this purpose a young "Victoria" Plum-tree was selected because this variety of Plum is particularly susceptible to attacks of Plum-Rust in this district. The Plum-tree was established in a large pot and fresh æcidiospores from the affected Anemones were placed on the upper and lower surfaces of a number of leaves, the whole plant being enclosed in a bell jar after the inoculations had been made. Certain leaves were left uninoculated as controls. Three weeks later, twenty-three of the leaves thus inoculated were found to bear on their under surface uredo pustules of the Plum-Rust, whereas the control leaves shewed no sign of the Rust. It is thus clear that *Æcidium punctatum* is a stage in the life-history of the Plum-Rust as it occurs in England, as well as in Russia and the United States.

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[1] Tranzschel, W.: Arbeit. der Kais. St. Petersburg, Nat. Ges., 1904.

[2] Quoted in Duggar's "Fungous Diseases of Plants," p. 418.

During the last two years there have been severe epidemics of Plum-Rust in the fruit-plantations of Cambridgeshire, the attack last year being so severe as to cause premature defoliation of a large number of trees. Hitherto there has been doubt as to the manner in which the Plum-Rust survives the winter in this country. Both uredospores and teleutospores are produced on Plum-leaves affected by this fungus. Experimental proof is lacking that the sporidia formed by the teleutospores or resting spores which survive the winter can infect the leaves of the Plum the following season. Indeed such a result is improbable now that we know that the Plum-Rust is a heterœcious Eu-form, for the function of the sporidia is to infect species of Anemone. It is likely, however, that the uredospores from a means by which the fungus may survive the winter, for Tranzschel has shewn that uredospores of the Plum-Rust kept over the winter at St. Petersburg are capable of germinating the following season. But it is yet uncertain whether this is a frequent means of propagation from season to season. Furthermore, if re-infection the following year were due exclusively to uredospores formed in the previous year one would rather expect Plum-Rust to develop soon after the foliage had appeared, whereas Plum-Rust is frequently not in evidence until the summer season is well advanced.

The experiments detailed above shew that there is another means by which this fungus can survive the winter and cause infection the following year. *Anemone coronaria* is a plant frequently found in gardens and the mycelium of *Æcidium punctatum* is perennial in its tissues. Thus a plant of *Anemone coronaria*, once it has been affected by this rust, gives rise to crops of uredospores year after year, so that a few plants attacked by this æcidium are sufficient in themselves to account for the recurrence of Plum-Rust year after year. After the first crop of uredospores of the season has been produced on Plum-leaves there is every facility for the fungus to spread, because by analogy with other Rusts, successive crops of uredospores may be produced about every fortnight under favourable conditions.

It is obvious that the eradication of plants of *Anemone coronaria* affected by this æcidium will be of assistance in the control of this very common Rust.

June, 1911.

NOTES ON RECENT LITERATURE.

RECENT WORK ON ŒNOTHERA.

THE remarkable genetical phenomena exhibited by the species of Œnothera are stimulating a rapid production of papers on various aspects of the subject, which is fast passing beyond the reach of any but specialists.

Professor H. de Vries[1] has published a preliminary account of experiments in hybridising *Œ. biennis* and *Œ. muricata.*[*] The offspring of the first cross between these species differs according to the way in which the cross is made: in both cases the hybrid markedly inclines in appearance towards the pollen parent. The hybrid from each cross, when self-fertilised, breeds absolutely true for an indefinite number of generations.

The two hybrids may be designated as (M ♀ B ♂) and (B ♀ M ♂) respectively. They may be crossed together in two reciprocal ways, and from such crosses de Vries obtained the following remarkable results. The cross (M ♀ B ♂) ♀ × (B ♀ M ♂) ♂ gave offspring which corresponded absolutely with *muricata*, shewing no trace of the characters of *biennis*. The reciprocal cross (B ♀ M ♂), ♀ × (M ♀ B ♂) ♂ gave pure *biennis* free from all signs of *muricata*.

It will be seen that in both cases the characters which appear in the offspring are those handed on by the same sex as that by which they were introduced in the original *muricata-biennis* cross. For example, in the cross (M ♀ B ♂) ♀ × (B ♀ M ♂) ♂ the mother received the *muricata* characters from her mother, and the father received the *muricata* characters from his father: the offspring is *muricata*. The same applies, *mutatis mutandis*, to the reciprocal cross producing *biennis*. "The characters of the grandfather cannot be transmitted to the grandchildren by the mother; nor can those of the grandmother be transmitted to the grandchildren by the father." (p. 99).

The conclusion is that the pollen grains and ovules of a plant carry different sets of characters, so that B ♀ × M ♂ is really a different cross from M ♀ × B ♂. The conception of the different hereditary content of pollen and ovules is familiar through the work of Miss Saunders and Mr. Bateson on *Matthiola*[2] and earlier studies of de Vries on *Œenothera nanella*[3]: but the present instance is novel in several respects, the most curious being that this "heterogamy" (as de Vries rather unfortunately calls it) here occurs in pure species. It is shown that the characters transmitted by the pollen of *biennis* are closely similar to those typical of the external form of the species; those borne by the ovules are of a quite different type, which attains more or less complete expression in hybrids with *biennis* as the mother: the same applies to *muricata*.

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[*] When referring subsequently to species of *Œnothera* the generic initial will be omitted.

[1] "Über doppeltreziproke Bastarde von *Œ. biennis* und *Œ. muricata*." Biol. Centralbl. XXXI., p. 97, Feb., 1911.

[2] Report IV. to the Evol. Comm. of the Royal Soc., pp. 5, 36; 1908.

[3] "Über die Zwillings-bastarde von *Œ. nanella*." Ber. d. d. bot. Ges., XXVIA., p. 667; 1908.

Many other crosses between the species and their hybrids have been carried out, and confirm the explanation advanced: and similar phenomena have been found to occur in crosses between *biennis* and several other species of Œnothera. The phenomena of "heterogamy" are explained by a theory of segregation of characters combined with selective sterility of half the ovules and pollen grain. Sterility of 50% of the ovules and pollen grains has been shewn to occur widely in Œnothera spp.,[1] but there is as yet no experimental proof of the theory of selective sterilisation, however probable such may appear.

The suggestion that *Œnothera Lamarckiana* is of hybrid origin has frequently been made to account for part of its remarkable mutability. M. Leclerc du Sablon[2] has constructed a theoretical scheme in terms of known facts of Mendelian inheritance, gametic coupling, etc., by which the appearance of occasional "mutations" would be produced among the offspring of a hybrid plant. On the practical side, Dr. Bradley M. Davis[3] has published results which shew that plants bearing a striking external resemblance to *Lamarckiana* can be produced by crossing *biennis* with *grandiflora*: his second paper contains detailed descriptions, drawings, and photographs. Davis found, however, that the hybrids shewed a great amount of segregation in F_2, and in this important respect they differ from the *Lamarckiana* grown by de Vries and others, which shews only occasional deviations from type. Further, the theory of the hybrid origin of *Lamarckiana* from *biennis* and *grandiflora* fails to give any probable interpretation of the appearance of such striking mutants as *nanella* the dwarf, *gigas* with its double number of chromosomes, and possibly also the pollen-sterile *lata*: though it may be conceded that at least the two first are sports of types not comparable with such forms as *scintillans* and *rubrinervis*. *Gigas* can be paralleled elsewhere, and does not imply hybridisation: it is on the production of such forms as *rubrinervis* that evolution chiefly depends, according to the mutation theory; and it is precisely these forms which are open to suspicion as being products of segregation among characters blended by hybridisation.

In this connection the historical evidence is important. It appears that the *Lamarckiana* used by de Vries is related to plants grown by Messrs. Carter & Co., of London, about 1860.[4]

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[1] J. M. Geerts. "Beiträge zur Kenntniss der Cytologie und der partiellen Sterilität von *Œ. Lamarckiana*. Récueil Trav. Bot. Néerlandais: V., p. 93, 1909.

[2] "De la nature hybride de l'Œnothère du Lamarck." Rév. gén. Bot. XXII., p. 266, 1910.

[3] "Genetical Studies on Œnothera. I.—Notes on the Behaviour of Certain Hybrids of Œnothera in the First Generation." Amer. Naturalist XLIV., p. 108, Feb. 1910. II.—"Some Hybrids of *Œ. biennis* and *Œ. grandiflora* that resemble *Œ. Lamarckiana*." *Ibid*, XLV., p. 193, Apr. 1911.

[4] De Vries. "Über die Dauer der Mutationsperiode bei *Œ. Lamarckiana*." Ber. d. d. bot. Ges. XXVIa., p. 382, 1905.

Davis shows that about this time *grandiflora* was cultivated in England by Thompson, of Ipswich; the evidence being a single sheet in Dr. Asa Gray's herbarium at Harvard. It will be of great interest if any connection is established between *grandiflora* and Messrs. Carter & Co. at that period.

J. A. Honing[1] has compared by means of careful measurements the "twin hybrids" *læta* and *velutina* (produced in F_1 of the crosses *biennis* ♀ × *Lamarckiana* ♂ and *biennis* ♀ × *rubrinervis* ♂) with *Lamarckiana* and *rubrinervis* respectively. His researches show that the *læta* hybrid has preponderating *Lamarckiana* characters, the *velutina* hybrid preponderating *rubrinervis* characters. The conclusion is drawn that the plants of these species are "double individuals," the *Lamarckiana* having *rubrinervis* characters latent, the *rubrinervis* having *Lamarckiana* characters latent: these latent characters being revealed in crosses with *biennis* (or *muricata*). The theory is difficult to understand in that it is not elucidated by any scheme of a Mendelian nature: when the author says that by "double individuals" he means what others mean by the word "hybrid" it seems that he is straining the normal use of the word. The study, however, is of much interest in relation to other work on the possible hybrid origin of the *Lamarckiana* group of forms, and on the differing genetic content of pollen grains and ovules.

H. H. Zeijlstra[2] has shown that the well-known dwarf species described by de Vries and others as *nanella*, contains in local patches of the stem, and especially in the secondary wood, dark masses of a substance, which he interprets as the zoogloeæ of a species of Micrococcus: these sometimes cover as much as one-eighth the area of a transverse-section. To the presence of this supposed parasite is attributed certain features, hitherto regarded as typical of *nanella*, and giving it a diseased appearance—*viz.* the distortion of the leaves, the crookedness, imperfect unfolding and more or less marked sterility of the flowers. Rigorous proof, however, is not given for this statement; for not only is the identification of Micrococcus not critical (at least as described). but inoculation experiments were not performed, and artificial cultures of the organism are not mentioned; nor is information given as to the presence or absence of the dark masses in other species of Œnothera. "Normal" dwarfs occasionally arise, these differing from *Lamarckiana* chiefly in size: and "diseased" plants sometimes produce "normal" branches. The "diseased" condition is well-known to be transmitted to the offspring both by ovules and pollen-grains.

R.H.C.

[1] "Die Doppelnatur der *Œ. Lamarckiana*." Zeits. f. Ind. Abst.-u. Vererbungslehre, IV., p. 227, 1911.

[2] "*Œnothera nanella* de Vries, eine krankhafte Pflanzenart." Biol. Centalbl. XXXI., p. 129, 1911. Also Proc. Roy. Acad. of Sci., Amsterdam, Dec. 24th, 1910, p. 680.

GRAFT-HYBRIDS.

THE classical cases which have been cited as examples of graft-hybrids[1] are well known to everyone. These intermediate or hybrid types, described as being of vegetative origin, had, however, only been produced in rare and isolated cases, and none of the persistent attempts to secure a repetition of the phenomenon had met with any success. The nature of these forms and the manner of their origin therefore provided a fertile field for debate, which, however, was productive of little positive result.

But within the last two or three years notable progress has been made towards a solution of the problems of graft-hybridism. The starting point was Winkler's success in inducing the development of graft-hybrids between the Tomato and the Black Nightshade.

Winkler[2] found in *Solanum* a genus of plants which, under suitable treatment, very readily produce adventitious shoots Not only so, but the development of these shoots can be localized at a desired point. Reciprocal grafts were made between seedlings of the Tomato and the Nightshade. The grafts having been given time to become established, the plants were cut through transversely in such a way as to expose the newly joined tissues of scion and stock at the cut surface.

Adventitious shoots developed from the callus formed over the cut surface. The majority of these shoots had their origin in tissue belonging entirely either to the scion or to the stock. Such shoots merely reproduce the pure species from whose tissue they originated. But other shoots had their origin exactly upon the line of junction between the tissues of the two graft-symbionts; in such shoots the characters of the two species are combined in various ways.

In the simplest case[3], the tissues of the two graft-symbionts are united side by side so as to build up a single shoot, of which one side is pure Tomato, the other pure Nightshade. The contrast between the stiff hairs and divided leaves of the Tomato and the almost glabrous, simple-leaved Nightshade gives these "sectorial chimæras" a sufficiently striking appearance.

But in addition to the sectorial chimæras, Winkler[4] also obtained adventitious shoots which were intermediate in general habit between the two pure species. In all five, distinct intermediate types have now been obtained, each representing a different combination of the characters of the Tomato and the Nightshade,

In general character and behaviour, these types are exactly

[1] See Darwin (6), Strasburger (10), Noll (8). With regard to Darwin's cases of the transference of chlorosis through grafting, see Baur, "Über infektiöse Chlorosen, etc.," Ber. d. Deutsch. Bot. Gesell., XXV., p. 410.

[2] Winkler (11).

[3] Winkler (11).

[4] Winkler (12) and (13).

analogous with the earlier known graft-hybrids. Thus, among their axillary and adventitious shoots, one not uncommonly finds complete reversions to one of the pure species, as well as chimæras, in which the pure species is united with the intermediate type; or again, one intermediate type may give rise to one or more of its fellow types. In this last respect they of course differ from those graft-hybrids of which only one form exists, but an analogous case is to be found in the *Cratægo-mespilus* hybrids of Bronvaux, of which two distinct types exist.[1]

Winkler's results, which have been repeated and extended to other species of *Solanum* by Heuer[2], have established the fact that shoots of an intermediate type may be produced as a result of the vegetative process of grafting. The clue which led to an explanation of the phenomenon came from Baur, as a result of his experiments on *Pelargonium zonale*.[3]

Baur crossed a white-leaved race of this species with a green-leaved race. The hybrid seedlings were found to consist of green and white parts arranged in a mosaic. Some of these seedlings give rise to adult plants which are sectorial chimæras of green and white parts, exactly analogous to Winkler's sectorial chimæras of Tomato and Nightshade. The boundary between the white and green parts in the stem of a sectorial chimæra is often radial, but in some cases it follows a line such that one or two cell-layers of, say, white tissue overlie the internal green tissue. Such plants bear leaves with white margins and, as their anatomical structure shows, they are chimæras in which the boundary between the two components is not anticlinical but *periclinal*.

When Winkler described the first *Solanum* graft-hybrid which he obtained, Baur[4] suggested that it might be a percilinal chimæra. This, and the subsequent suggestion that other so-called graft-hybrids might be of the same nature, has since been proved to be well founded.

Winkler[5] has shown that four of his types are periclinal chimæras; the four types represent the combinations to be obtained when either the epidermis alone or the *two* outermost layers may be derived from either species. Macfarlane's work suggested, what Baur[6] and Buder[7] have since confirmed, that, so far as one can rely upon anatomical evidence alone, *Cytisus Adami* consists of an epidermis of *C. purpureus* surrounding internal tissue of *Laburnum vulgare*. Baur has shown that in the two *Cratægo-mespilus* hybrids respectively, one or two peripheral cell-layers are derived from the

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[1] Noll (8).

[2] Heuer (7). Heuer obtained successful results with *S. Melongena* and with *S. dulcamara*, as well as with the two species used by Winkler. He gives a photograph (p. 435) of a sectorial chimæra of *S. lycopersicum* and *S. nigrum* bearing lateral shoots of five kinds—the two pure species and three intermediate types.

[3] Baur (1).

[4] Baur (2).

[5] Winkler (15).

[6] Baur (3).

[7] Buder (4.)

Medlar, the internal tissue being derived from the White-thorn. Daniel's[1] observations indicate that his Pear-Quince hybrid is also a periclinal chimæra, with the Pear internal.

The phenomenon, so common among these periclinal chimæras. of the spontaneous production of reversionary shoots appears to be due to some irregularity in the divisions of the meristem, the cause of which is unknown. The change of form often exhibited by the adventitious shoots produced as a result of wounding, seems to follow naturally enough upon the opportunities for a rearrangement of the components which are afforded by the death of certain cells and the rapid multiplication of others.

There remains one of Winkler's intermediate types which suggests further possibilities. Winkler finds that the germ-cells of this type (*S. Darwinianum*) possess twenty-four chromosomes,[2] the reduced number of the Tomato being twelve, that of the Nightshade thirty-six. Winkler therefore supposes that in this case a fusion must have taken place between the vegetative cells of the pure species, and that the sub-epidermal layer of the hybrid, at least, must be the product of this fusion.

At one time some acceptance was accorded to the idea that graft-hybridism, if it were a real phenomenon, must involve cell-fusions between the graft-symbionts. But the cytological studies of Strasburger[3] and Noll[4] lent no support to the hypothesis, the graft-hybrids which were examined being found to possess the same number of chromosomes as their respective parents; and though Nêmec suggested that an autoregulative process of reduction might take place, whereby the diploid number of chromosomes would be restored, there was little positive evidence in favour of his suggestion.

Further investigations into the origin of *S. Darwinianum* will be awaited with great interest, for at the present time it alone affords any positive indication that such cell-fusions may take place, giving rise to cells, and ultimately to tissues, which are essentially of a hybrid nature in contra-distinction to the tissues of a chimæra, which are pure to one species or the other.

Of the literature cited below, the works of Darwin, Strasburger and Noll provide general descriptions of the characters and putative origin of the earlier graft-hybrids; in them will be found references to a number of articles which need not be recapitulated here.

R.P.G.

[1] Daniel (5).

[2] Winkler (15).

[3] Strasburger (10).

[4] Noll (8), p. 37.

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GANONG BOTANICAL APPARATUS.

A CATALOGUE of apparatus for use in plant physiology issued by the Bausch and Lomb Optical Co., and a first supplementary list are to hand. In them Prof. Ganong describes a number of pieces of apparatus devised by himself and made by Bausch and Lomb under his direction. They are intended primarily for demonstration and class purposes. Ganong has paid special attention to simplicity of construction and convenience of manipulation; and in these respects he appears to have attained a considerable measure of success. The apparatus is, on the whole, simple and ingenious, and would no doubt prove quick and easy to use. On the other hand the cost is, in some cases, prohibitive. Few laboratories could afford the luxury of the Autographic Transpirometer and Balance, costing in all about £40; and it may be doubted whether considerations of expense will allow of the ready adoption for class use of much of the other apparatus in place of rough and ready forms which can be made at small cost from materials available in a laboratory. For instance, when quite good starch photographs can be made and similar experiments performed with the aid of wire gauze and black cloth, with strips of sheet lead as clips, there is not likely to be much demand for a two guinea apparatus: the latter allows of more ready diffusion of CO_2, but, as Ganong himself says, "this is only a matter of degree."

The catalogue is nevertheless worth a careful perusal by all who are interested in the teaching of plant physiology. We may mention, especially, the potometer, a modification of the form with horizontal capillary, and the manometer, for root pressure experiments; both reasonably cheap, and having distinct advantages. The wheel space-marker for marking off equal lengths along roots etc. in growth experiments is a decided improvement on the camel hair brush both in efficiency and economy of time. The leaf-area cutter for use in connexion with Sachs' dry weight method is neat; but must be used with certain precautions to ensure trustworthy results (see Brown and Escombe, Roy. Soc. Proc., 1905, and Thoday, Roy. Soc. Proc., 1909, where a similar instrument is described). It would be an improvement if the leaf-discs received final drying in a tube which could be closed during weighing, as their leaf substance is frequently hygroscopic. The temperature stage has also much to recommend it, but it is difficult to see why it should not be quite as effective in a much cheaper form.

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FLORAL EVOLUTION: WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

BY H. F. WERNHAM.

IV. TETRACYCLIDÆ: PART I. CONTORTÆ.

THE Pentacyclidæ, we have found, reflect the earliest evolutionary "efforts" in the direction of sympetaly, and so bear many marks of their archichlamydeous origin, particularly in regard to the numbers of the parts and cohesion of the petals. In the Tetracyclidæ, on the other hand, the stamens alternate with, and never exceed in number, the corolla segments; the gynæcium is in the majority of the species bicarpellary; and the petals are almost invariably united to form a tube. In other words, the primary principle of economy has reached its highest expression, and sympetaly, the fundamental step in the direction of adaptation to insect-visitors, is established practically without exception; we anticipate, therefore, that the guiding principle of evolutionary progress which we shall observe among the Tetracyclidæ will be further adaptation to insect-visits. This adaptation may take a very special and complex form, as in Contortæ (Asclepiadaceæ); or it may be of such extensive occurrence as to represent a general evolutionary tendency, as in the case of the zygomorphy of the Tubifloræ and the aggregate inflorescence of the higher Campanulatæ. The latter, moreover, display a special advance in their so-called "pollen-presentation" mechanism.

The fundamental lines of advance in the direction of adaptation to insect-visitors are associated with certain tendencies which we have already referred to as *secondary* economy tendencies. Thus, sympetaly becomes associated with epipetaly, as we have seen already among the Pentacyclidæ. Zygomorphy, we shall observe, is followed by oligomery of the andrœcium, undoubtedly with relation to the entry of the insect-visitor into the flower. Aggregation of florets is followed by reduction of the calyx, usually to a pappus; the protective function in the capitulum is discharged by the mutual protection afforded by the closely aggregated florets, and also by the common involucre; the calyx is thus available and utilized for another function, *viz.*, that of fruit-dispersal.

Economy in production of megasporangia, we have seen,[1] is not an extensive tendency among Archichlamydeæ; it seems, however, to constitute a marked feature of the Tetracyclidæ, the ovary in the highest forms—comprising nearly 30% of the total number of species—being uniovulate, with one fertile loculus only (Asterales of Bentham and Hooker). A single ovule in each loculus of a bi- or multi-locular ovary characterizes some Contortæ, a large section of Tubifloræ, and many Rubiales.

CONTORTÆ.

The natural orders of this group, together with those comprised under Engler's Tubifloræ, have been designated *Bicarpellatæ* by Bentham and Hooker, in virtue of the fact, with very rare exceptions, the ovary is in all cases bicarpellary. A similar condition obtains in the most advanced members both of Archichlamydeæ (Umbelliferæ) and of Sympetalæ (Compositæ), so that fully three-quarters of the species in the latter series have a bicarpellary gynæcium. We are led to the conclusion that this condition represents the highest expression of the economy principle in so far as the gynæcium is concerned; and it is found very generally, we should mention, even where the ovary is unilocular and uniovulate. In the Bicarpellatæ, however, the unilocular ovary is a decided exception.

The cohort Contortæ of Engler is coincident with the Gentianales of Bentham and Hooker, and includes the natural orders Oleaceæ, Salvadoraceæ, Loganiaceæ, Gentianaceæ, Apocynaceæ, and Asclepiadaceæ; these Orders are identical in name and composition in the two systems. Their typical essential characters are displayed in the annexed table.

With the curious exception of the Oleaceæ, the stamens are invariably isomerous and alternate with the corolla-segments in this cohort; in the Oleaceæ economy has proceeded to the degree of an andrœcium of two stamens only.

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[1] Supra, p. 113.

The exceptions to the bicarpellary pistil are very few in number, amounting to barely 25 species in all—*i.e.*, about 0·6%—and occurring in Oleaceæ (*Nyctanthes*, *Fontanesia*); Apocynaceæ (*Lepinia*, *Notonerium*, *Pleiocarpa*); and Loganiaceæ (*Labordia*, *Pagamea*, *Desfontainea*).

CONTORTAE (GENTIANALES)

Order	Approx. no. of species.	Corolla	Stamens	Pistil		
				Carpels	Loculi	Ovules per loculus.
OLEACEAE	390	(4) usually; rarely free	2 rarely 3–4	(2) rarely 3	2	1–2
SALVADORACEAE	6	4 usually sub-free	4	(2)	1–2	1–2
LOGANIACEAE	350	(4–5)	C rarely 1.	(2)	2–1	∞ or 1
GENTIANACEAE	750	(5)	C	(2)	1 usually	∞
APOCYNACEAE	1000	(5)	C	(2) rarely more	2–1	∞ – few – 1
ASCLEPIADACEAE	1300	(5)	C	(2)	2	∞

In a good many Apocynaceæ the two carpels are apocarpous or sub-apocarpous, being united under a common style; in view of their advanced position among the Angiospermæ taken as a whole, this condition will be readily regarded as secondary, a specialization having relations with fruit-formation and seed-dispersal. A tendency to the unilocular state of the ovary finds expression in some Salvadoraceæ, and a few Loganiaceæ and Apocynaceæ; in Gentianaceæ a unilocular ovary is the rule.

As regards the number of ovules, the Oleaceæ and Salvadoraceæ have one or two per loculus; for the rest, the number is usually indefinite. In the Apocynaceæ a tendency to economy in this respect is traceable, about 12% of the species having four ovules or less to each carpel; in Loganiaceæ about 11% of the species have but a single ovule in each loculus of the ovary.

Turning now to the degree of advance on general lines in regard to the reception of insect-visitors, we find in the first place that the traces of polypetaly are extremely few and of doubtful significance, being confined to the Oleaceæ and Salvadoraceæ. Of the former order the petals are distinct, or loosely united in pairs, in *Linociera* and its allies *Chionanthus*, *Notelæa*, and *Noronhea*; among Salvadoraceæ *Dobera* and *Azima* have polypetalous corollas, and these represent some six species out of eight. We shall return to this point when we approach the question of the affinities of the group. The sympetalous corolla, then, is a character almost invariable for the Contortæ.

The stamens are nearly always epipetalous, the hypogynous arrangement occurring only in a few Oleaceæ and in Salvadoraceæ. There is little or no tendency either to aggregation into dense inflorescences or to zygomorphy; but there is a special tendency to gynandry in relation to insect-visits, observable in the Apocynaceæ and culminating in the Asclepiadaceæ. This gynandry is associated in the latter order with other specializations such as massing of its pollen, so that the floral complexity of the Asclepiads is comparable only with that found in the Orchids.

Epigyny is practically non-existent among the Contortæ, partial exceptions being afforded by a few Apocynaceæ (e.g., *Apocynum*, *Ichnocarpus*, *Epigynum*); in these the ovary is more or less sunk in the receptacle, in a manner comparable with the semi-inferiority found in the sapindalian Celastraceæ.

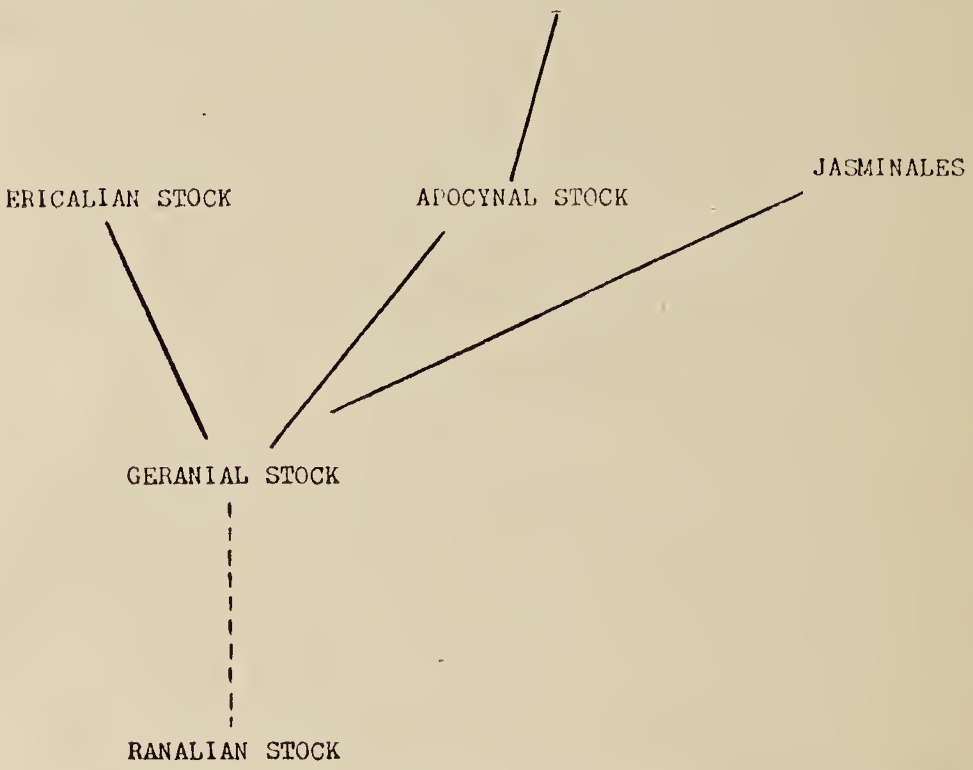
We have now to consider the question of the ancestry and affinities of this cohort, and we are met at the outset with a difficulty which did not present itself so formidably in the case of the Pentacyclidæ. This difficulty finds expression in the remarkable constancy of the essential floral characters throughout the group, and in the relatively advanced degree of those characters considered from the aspect of our two fundamental evolutionary principles. A gulf is thus discovered between the Contortæ and the Archichlamydeæ which at first sight seems difficult to bridge; for the combination of an isomerous alternating andrœcium with a bicarpellary and superior ovary is extremely rare in the latter series—the sole group in which this combination occurs at all to any extent being the highly evolved Umbellifloræ, in which the ovary is inferior.

In the Archichlamydeæ, however, we must contemplate the tendency to economy from the aspect of its progress rather than of its realization; and the rarity of forms which have fully worked out this tendency before adopting sympetaly is scarcely matter for surprise. For the ancestry of the Contortæ we must look for a group in which a tendency to isomery of the andrœcium is definitely traceable, together with a tendency to a bicarpellary gynæcium; at the same time any tendency to epigyny must be absent, or practically absent. These conditions are satisfied by the stock represented in the Geraniales-Sapindales plexus, and by no other. Examples of isomery of the androecium and alternation of stamens with petals are to be found in all the larger natural orders of Geraniales and Sapindales—in the latter, the more advanced cohort, more frequently than in the former. A bicarpellary ovary is not of such common occurrence; but examples are forthcoming in most of the larger orders, while in the D section of Geraniales, including the Polygalaceæ, the pistil is nearly always composed of two carpels.

Unfortunately, however, the Contortæ have left no traces of their progress from polypetaly to sympetaly in the shape of pentacyclic forms; neither a second staminal whorl nor any hint of it ever occurs. Nor can they be regarded as the direct descendants in any sense of a group so highly evolved as the Ericales, although these originated most probably from the same stock—the geranial. The Pentacyclidæ, we may premise, seem to have left no descendants among the Tetracyclidæ, although the latter have almost undoubtedly been derived from the same archichlamydeous stocks. The immediate antecedents of the Contortæ may have been polypetalous forms in which the economy principle had reached its limiting expression in an isomerous alternating androecium and a bicarpellary gynæcium; or they may have been pentacyclic and sympetalous, the tendency to economy being active, in association with a corolla-tube, until the typical Contortæ were evolved. In either case the intermediate forms have been extinguished.

We regard the Contortæ, then, as derived from the geranial stock, like the Ericales, on some such lines as indicated in the accompanying diagram; and we may suggest that while the latter have employed their evolutionary powers, so to express it, in the direction of specialization of habit and details of floral structure, the Contortæ have reserved their efforts for the realization of the economy tendency. This refers, of course, to the passage from polypetaly to sympetaly; we have now to consider the question of evolution and affinities within the group itself.

We need first to search for those members of the cohort which are nearest to the archichlamydeous stock—in other words, we must endeavour to find those members which are relatively primitive; and it is at this stage that we feel with particular keenness the disadvantage of the evolutionary break to which we have drawn attention above. A pleiomerous androecium we cannot find; a gynæcium with more than two carpels occurs so rarely that very little significance must be attached to it, unless this can be associated with other considerations. Polypetaly, or an approach to it, occurs only in the Oleaceæ and Salvadoraceæ, two groups apparently allied together, but isolated, we shall see, from the rest of the cohort.



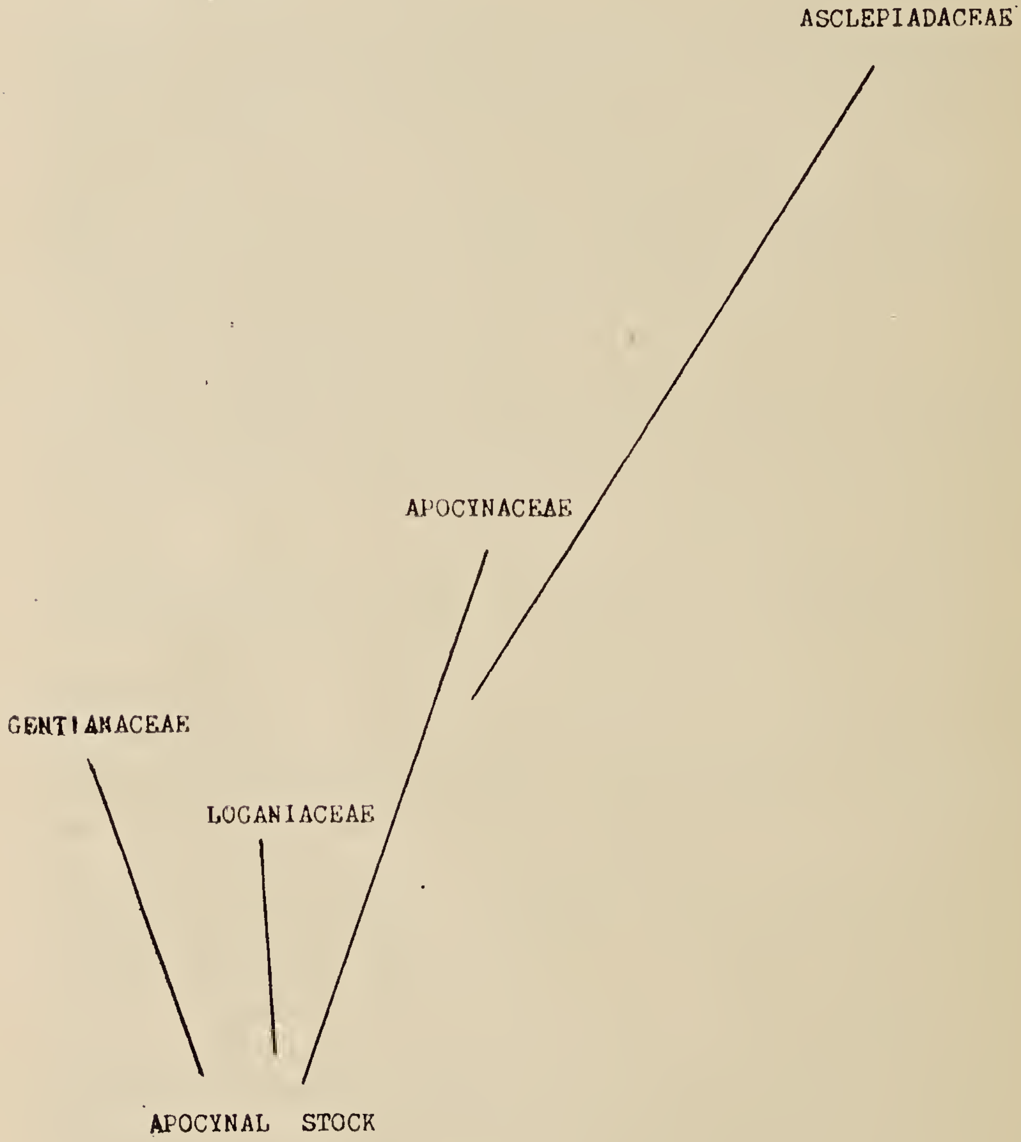
Let us consider for a moment the *habit* of the plants concerned. The Oleaceæ, Salvadoraceæ, Loganiaceæ and Apocynaceæ are for the most part arborescent or fruticose; Gentianaceæ and Asclepiadaceæ are mostly herbaceous or suffruticose. The extensive occurrence in a group of the herbaceous habit, particularly when combined with constancy in numbers in the essential organs, seems to be a more or less reliable indication of high evolutionary advance—as witness the Compositæ, the Grasses, the Orchids, and, significant in the present connection, the Asclepiads. Such groups, it may be urged, owe much of their success in the struggle for existence to their modest demands for space, while their slender equipment against external severities is compensated by subtleties of structure and habit, vegetative and reproductive.

Indeed, in so far as the herbaceous habit is associated with small requirements in the matter of space and the necessity for relatively little output of energy to attain maturity, it has a broad biological significance, and may be regarded as the expression of a definite evolutionary tendency. Not only the Angiosperms, but the whole series of vascular plants, provide abundant evidence in support of the existence of such a tendency: one need only mention the giant Calamarieæ and Lycopodiales in comparison with their reduced descendants. Reduction in size of the individual, coupled with increase in efficiency of detailed structure, seems, in fact, to be a general principle of descent, in both animal and vegetable kingdoms. In any case none will deny to the Asclepiadaceæ a place of highest specialization among the Contortæ. The Gentianaceæ are not so obviously advanced; but the constancy of floral character throughout the group, the characteristic habit—almost invariable glabrousness coupled with a generally rigid, stiff appearance easier to recognize than to describe—and a definite tendency to the unilocular condition of the ovary, all point to this order as being, at any rate, not relatively primitive.

Of the remaining orders the Loganiaceæ and Apocynaceæ are those which, we have seen, shew the greatest amount of variability among the Contortæ—little though this may be; and it is to these orders that we are led to assign the position of greatest proximity to the ancestral archichlamydeous stock. Among these two orders, as we have already remarked, we find a few traces of the multilocular ovary; but it is in the number of ovules that they appear to display a definite evolutionary tendency—namely, to economy in ovule production. This will be a matter of significance when we approach the question of the origin of the Tubifloræ. In the Apocynaceæ, again, we find much more variability in leaf-arrangement than in the other orders, in which opposition of the leaves is a remarkably constant feature.

The Apocynaceæ and Loganiaceæ are not readily separable on grounds of broad evolutionary tendencies, and there seems to be little doubt that they both arose from a comparatively recent common ancestor. Each has progressed upon a special line; the Apocynaceæ, with the tendency of their to approximation stamens and adhesion to the stigma, and with their more or less specialized mechanism for seed-dispersal, seem to be on the whole more advanced than the Loganiaceæ. The higher Apocynaceæ, in fact, pass by way of a series of transitional forms into the Asclepiadaceæ, the two orders being connected by the tribe Periploceæ of the latter, in which the filaments are free, or almost so, and the pollen granular. These higher Apocynaceæ, although not herbaceous, are mostly slender climbing shrubs, with a general habit closely resembling many Asclepiads.

The recent (sympetalous) common ancestor of the Apocynaceæ and Loganiaceæ we may name the contortal or apocynal stock. From this the latter order represents a relatively short side-branch, with economy in ovule output as a leading tendency. The Apocynaceæ terminate a longer branch (see annexed diagram), determined by specialization for seed-dispersal, by gynandry, and by reduction in ovule-number. Before the development of the last-named tendency a side-branch emerged from this apocynaceous line, the guiding principle of which was the further elaboration of the gynandrous tendency, coupled with aggregation of the pollen, thus producing the complexities of the Asclepiadaceæ; in the latter, moreover, the specializations in fruit and seed foreshadowed in Apocynaceæ—secondary apocarpy and comose seeds—have become practically constant characters.



We shall regard the Gentianaceæ as lying upon a third line emanating from the "apocynal stock," the determining tendencies being to the herbaceous habit, and to the unilocular condition of the ovary.

There remain for consideration the Oleaceæ and Salvadoraceæ. While it is among these two natural orders alone of the cohort that we find examples of polypetaly, they display remarkable advance in the nearly constant character of having but one or two ovules in each loculus of the ovary, which is almost invariably bi-carpellary. In the Salvadoraceæ, comprising less than a dozen species, the andrœcium is tetramerous—*i.e.*, isomerous with the corolla; in Oleaceæ, represented by nearly 400 species, the stamens are two in number, with rare exceptions.

This occurrence of oligomery of the andrœcium throughout an extensive group in which the flowers are regular is without parallel in the whole series of flowering plants. One can only suggest that the case of the oleaceæ represents a special extension of the primary economy tendency, unassociated with any corresponding adaptation, on broad general lines, to insect-visits.

It seems, therefore, in any case, that we must regard the Oleaceæ as relatively advanced, and that we must not lay too much stress upon the indications of polypetaly which they display. Taken in consideration with the other floral characters this polypetaly may not impossibly be secondary, as also in the Salvadoraceæ, in which order a dialypetalous corolla and a hypogynous andrœcium characterize most of the few species. It is, at the same time, quite possible to regard this polypetaly as primitive, without viewing these two orders as primitive on the whole relatively to the rest of the Contortæ. Their extreme advancement on the line of economy in production of parts, in fact, has led the writer to regard them as so far isolated that they may claim the rank of a separate cohort, which might suitably be named the *Jasminales.* For they differ essentially in most of their characters, in addition to those already mentioned, from the typical derivatives of the apocynal stock. Contorted æstivation of the corolla is of such very general occurrence among these latter as to have suggested Engler's cohortal name—Contortæ; in Oleaceæ and Salvadoraceæ the æstivation is prevailingly imbricate. The relatively frequent occurrence of compound leaves among Oleaceæ (*Jasminum*, *Fraxinus*) is another exceptional feature —and is, indeed, exceptional for all sympetalous shrubs and trees, which usually have simple leaves.[1] A further sign of advance in this group, and of considerable interest from the general standpoint of evolutionary progress, is the appearance of what may be named

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[1] Apart from Oleaceæ, the Bignoniaceæ, and the genus *Vitex* of Verbenaceæ, are the only important exceptions to this statement.

"apetaly." Examples of flowers with but a single whorl of perianth are afforded by the ashes (*Fraxinus*), and by the genera *Forestiera* and *Olea*; these examples seem to possess no little importance as suggesting the possibility that many of the "Apetalæ" may have originated similarly by degradation from sympetalous ancestors.

In view of the foregoing considerations, we are led to regard the Jasminales (*supra*) as representing a terminal point on a line of descent separate from that of the apocynal stock which branched off from the latter line somewhat as indicated in the diagram on p. 222. The apocynal stock and its immediate derivatives, we shall see on the other hand, do not appear in any sense to represent a terminal evolutionary point, for we shall find many reasons in favour af connecting them by a series of transitional forms with the important group Tubifloræ, which now presents itself for our consideration.

(*to be continued*).

PRELIMINARY OBSERVATIONS ON THE ECOLOGY OF *CALLUNA VULGARIS* ON THE WILTSHIRE AND BERKSHIRE DOWNS.

By M. C. Rayner, B.Sc. and W. N. Jones, M.A.,

Soil Analyses by J. W. Tayleur, B.Sc.

CALLUNA VULGARIS, associated with other more or less typical heath plants, occurs sporadically on the chalk-downs of the South of England, sometimes in sufficient abundance to form a conspicuous feature of the vegetation.

In a few places on the Berkshire and Wiltshire Downs the heather grows luxuriantly to a height of 2—3 feet, giving rise to well-defined communities from which the characteristic plants of the surrounding vegetation are excluded; more often it occurs mixed with grasses and other species, some of which are alien to the typical Down flora of the neighbourhood.

This heath flora is found chiefly on the more elevated part of the Downs, often as high as, or above 700 feet, the distribution varying from scattered patches over large areas to smaller and very well-defined communities which contrast sharply with the surrounding vegetation, the tendency to spread being apparently determined by definite factors.

It seems probable from their distribution and association with the characteristic plants of the locality, that the heath plants are invaders, which in some cases, e.g., *Calluna*, can compete successfully with the original inhabitants.

The presence of these plants on the chalk uplands is apparently correlated with the fact that in Wilts and Berks, as elsewhere, the chalk is locally overlaid by clay-with-flints. A possibility of small tertiary outliers also exists, the upper beds of which form characteristic heaths and commons in other parts of Berkshire. Clay-with-flints is a general name for a superficial deposit, varying in character in different localities; in the district under consideration usually a heavy yellowish clay containing flints. Older observers regarded it as derived from weathering of the chalk (1). A more recent view holds that the material composing it was derived from outlying Eocene tracts during late Pliocene times, broken up and distributed in the glacial period, much having been since removed by erosion (2).

The deposit is a very local one, varying from a few inches to many feet in thickness, and is not always mapped in detail on the Drift Maps of the Geological Survey, but the contours of the areas occupied by *Calluna* often suggest the presence of clay-with-flints, and the present work confirms this.

Chemical analyses of clay-with-flints soils from the South Downs shew that they are usually deficient in calcium carbonate, but the deep rather heavy loam which is found in the area under consideration would not appear at first sight likely to favour the growth of a typical heath plant such as *Calluna vulgaris*, in competition with grasses, etc. The soil conditions are, in fact, the reverse of those recorded by most authors as favourable to *Calluna* elsewhere. It seemed possible that some edaphic factor other than calcium carbonate might have a determining effect, since areas, apparently identical as regards exposure and physical characters of the soil, occur without *Calluna*.

The present paper is preliminary to an attempt to investigate experimentally the causes determining the existence and spread of *Calluna* under the conditions described.

A small area, bearing a well-defined patch of *Calluna*, has been mapped on a large scale (4 yards=1 inch) and a number of excavations 4 feet square opened down to the chalk along two section lines X and Y (Fig. 1).

From the data thus obtained, the thickness and distribution of the clay-with-flints were determined; the soil conditions were carefully noted, and samples removed for analysis.

The mapped area lies on Upper Chalk between the 600 and 700 feet contour lines on the ridge of Chalk Downs which forms the northward facing escarpment of the Hampshire Downs about six miles south-west of Hungerford.

Along this ridge, from Inkpen Beacon, where it reaches a height of over 1,000 feet, westwards, the Survey Drift Maps do not record

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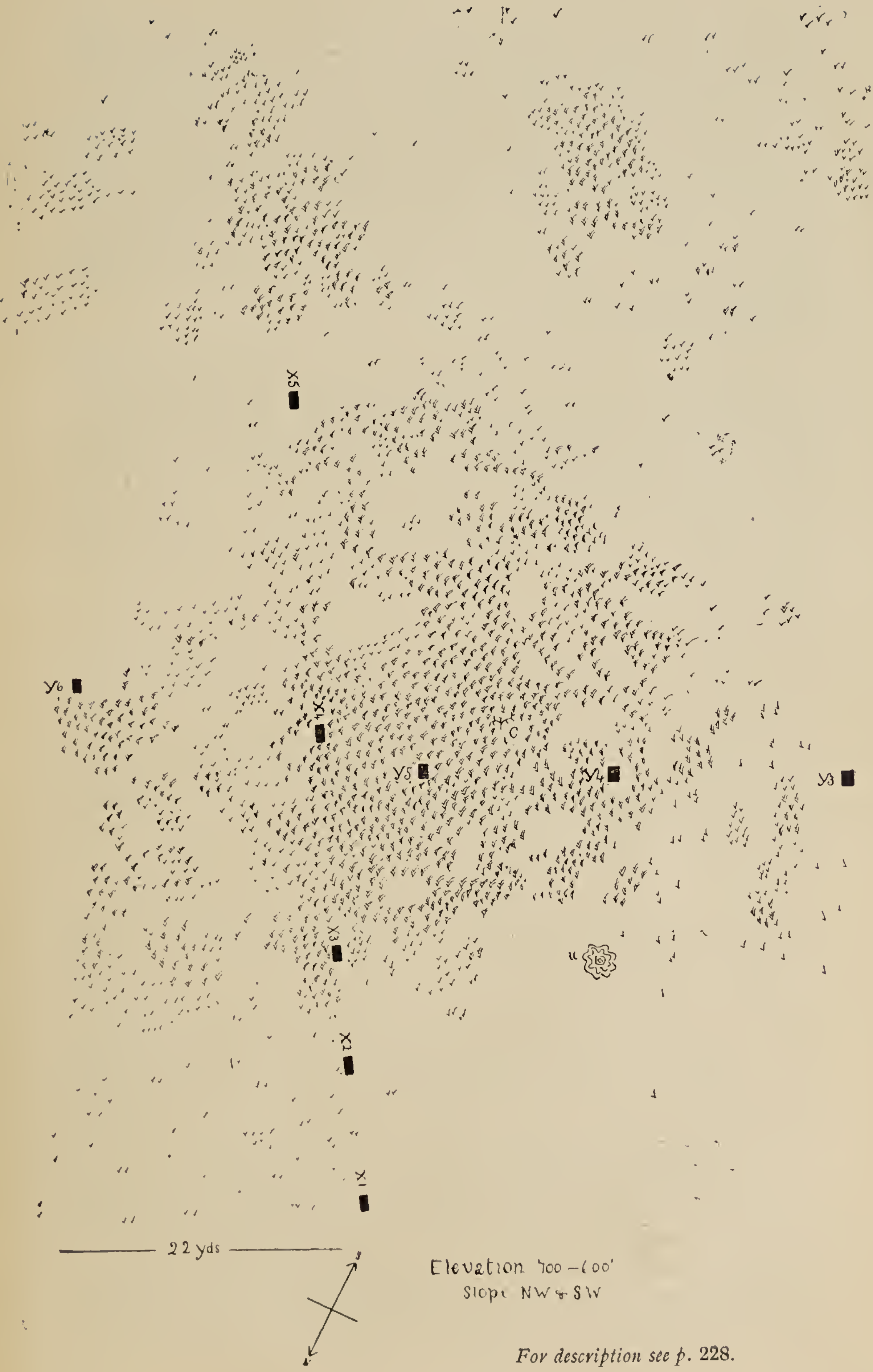
Fig. 1. Sketch-map, reduced from field-map, showing distribution of *Calluna vulgaris* on the area studied on Botley Down. The V-shaped marks indicate *Calluna* (single under 1 foot high, double over 1 foot high). The larger areas left blank are covered with grass. In the thick heather, indicated by continuous shading, grass does not occur (*e.g.*, between holes Y_4 and Y_5).

Five small patches of *Calluna* exist to the right of Y_3 (just outside the map) between Y_3 and Y_2.

U=*Ulex europæus*, C=*Cratægus monogyna*. X_1, X_2, &c., mark the position of holes. See Fig. 2 and Tables.



For description see p. 228.

clay-with-flints, but "loam" is marked at intervals, and the flora suggests that a cap of this nature extends to the edge of the escarpment, as *Ulex europæus*, *Cratægus monogyna*, and *Rubus Idæus* occur, growing with which the following herbaceous species have been noted—*Epilobium angustifolium*, *Epilobium montanum*, *Geranium Robertianum*, *Holcus lanatus*, and *Veronica Chamædrys*. A few sporadic plants of *Calluna* were recorded growing within twelve inches of such a typical chalk plant as *Helianthemum vulgare*. Further west, on Botley Down, *Calluna* becomes abundant with the distribution described.

Calluna has been established here for at least twenty years, and in spite of attempts to remove it, has shewn and still shews an inclination to spread. It is doubtful whether the land bearing it has ever been under plough, but there is arable land in the immediate neighbourhood.

Superficial examination suggests that in this neighbourhood the heather has picked out the more fertile soils, on which it has become established to the exclusion of the plants of the surrounding vegetation.

How the plants gain a foothold in the first instance, and how the spread is effected, constitute a distinct problem. Seed is freely produced and germinates readily, although rather slowly and irregularly. The seeds, however, are small, and the resulting seedlings extremely slow-growing. In pot cultures the development of the root system is slow and the seedlings are easily injured in the young stages. Ant heaps and mole hills are common on the surrounding Downs and often carry a rather distinct flora owing no doubt in part to the baring of the soil. These may afford the *Calluna* seedlings a starting point, although the surface is usually very dry during the spring and summer. Up to the present, seedling stages have not been observed either in such situations or on the downland in the neighbourhood of the mapped area.

Before recording the results of observations on the soil conditions with which *Calluna* is associated on the small area investigated, a summary of previous literature on the subject may be of interest.

Schimper (3) mentions *Calluna* as a typical heath plant, the only member of the family Ericaceæ which forms independent heath formations. It may form the chief constituent over large tracts of country if the soil is very poor in lime, on both sandy and moory stations, the former being physically, the latter physiologically dry. Schimper further notes that both sand and peat are very poor in mineral constituents, which probably favours *Calluna*, whose roots thrive *only in very weak nutrient solutions.*

Contejean (4) records *Calluna* as typically calciphobe, a view endorsed by Bonnier (5) as a result of his investigations on the flora of the Carpathians, Alps of Dauphiné, etc., but this author concludes from a comparison of these districts that, in the case of the majority of so-called calciphobe plants, the amount of lime present in the soil has only relative significance as a determining factor, its importance varying according to other local conditions.

De Candolle (6) records *Calluna* on very poor calcareous soil on the Muschel kalk.

Warming (6) mentions *Calluna* as a recorded calciphobe, incapable of growing in soils with more than ·02—·03% of lime. From his own observations he concludes that the plant is very accommodating and tenacious of life. "It can grow on the most sterile sand, which may be temporarily dry, or on wet boggy soil periodically dry."

"Though capable of growing upon moderately good soil, it seldom has the opportunity, because it is expelled by other plants. These latter, which are more exacting in their demands, avoid the more sterile and acid soil of heaths and resign it to ling."

Warming goes on to discuss the influence of lime on vegetation in general, and considers that it has been over-estimated. He refers to the experimental results of Graebner, who states that the significance of lime as a determining factor in the soil, depends on the poorness of the latter in other soluble mineral constituents.

Discussing the vegetative conditions which determine the growth of heath plants in North Germany, among which *Calluna* is mentioned as a typical member, Graebner summarizes his conclusions as follows:—"Ein unbedingtes Erfordernis für das Gedeihen der Heidepflanzen ist das Vorhandensein eines nährstoffarmen Substrates; sobald der Heide oder Heidemoorboden gedüngt wird, verschwindet die Heidevegetation ganz. Es ist nicht nur die auf nährstoffreicherem Boden den Heidepflanzen in der Gestalt der Pflanzenarten mit stärkerer Stoffproduction erwachsende Concurrenz, die Veränderung der Flora bedingt, sondern die Heidepflanzen sind auch thatsächlich, wie ich mich durch Cultur mehrfach überzeugt habe, nicht im Stande grössere Nährstoffmengen, die für andere Pflanzen noch gering erscheinen, zu verarbeiten." (7) p. 143.

With regard to the effect of lime the following is an extract from a more recent work by the same author (8), p. 236:—

"Bei den sogenannten kalkfeindlichen Pflanzen lässt sich das besonders in kalkreichen Substraten gut konstatieren, ja selbst die kalkfeindlichsten Heidepflanzen ertragen es, sogar die Sphagna konnte C. A. Weber fast alle in Kreide kultivieren und ich selbst zog Heidepflanzen in Kalkboden, wenn er nur nahrstoffarm war; wenn mit dem Kalk (wie fast überall in der Natur) reichlich Nährstoffe vorhanden waren gingen sie an Wurzeldeformation (Überfütterung) zugrunde; sie sind also bodenständig, weil auf anderen Bodenarten die Konkurrenz zu gross ist."

He alludes also to the extreme sensitiveness of these plants with regard to their water supply, a matter of some interest in connexion with the germination and establishment of seedlings mentioned above.

"Selbst auf den trockenen Heiden besitzt der Boden in der oberen humosen Schicht noch immer einen gewissen Grad der Feuchtigkeit, und sobald an einer Stelle durch Abholzung etc. ein vollständiges Austrocknen der oberen Bodenschichten herbeigeführt wird, sieht man *Calluna* absterben und verschwinden. Es macht sich diese Empfindlichkeit der Ericaceen z. B. auch sehr stark in der Cultur bemerkbar. Es ist eine jedem Gärtner bekannte Thatsache, dass, wenn eine Ericacee auch nur einmal ballentrocken geworden ist, sie gewöhnlich sehr schnell abstirbt" (7), p. 142.

The preliminary work on the soil conditions was undertaken with three objects in view:—

I. To determine the distribution and thickness of clay-with-flints, if present, and to estimate the amounts of $CaCO_3$ in the rooting area of the soils, inside and outside the heather area, and its effect on the distribution of *Calluna*.

II. By means of complete analyses, to determine the amount of available mineral matter in the soils.

III. To ascertain whether any edaphic factor (other than $CaCO_3$) is present which might favour the growth of *Calluna* or be inimical to that of other plants.

The following notes were made of the soil conditions in the holes along section line Y. The ground level rises gradually 20 feet 9 inches from Y_1 to Y_9.

Y_1. *Outside heather area.* Loamy soil over chalk. Chalk at 9 inches. Lumps of chalk within a few inches of surface. Soil fairly dry in wet weather.

Y_2. *Outside scattered heather patches.* Soil, passing into soil with flints, rather heavier below. Chalk at 15 inches. Small lumps of chalk within 6 inches of surface. Soil fairly dry in wet weather.

Y_3. *Inside scattered heather patches.* Soil, over soil with flints, coming clayey below. Surface of chalk rubble very irregular. Chalk at 17 inches. Soil rather wetter after rain.

Y_4. *In heather area.* Definite layer of clay-with-flints over chalk rubble, which in places comes within 12 inches of surface. Chalk at 31 inches. Soil retentive after rain.

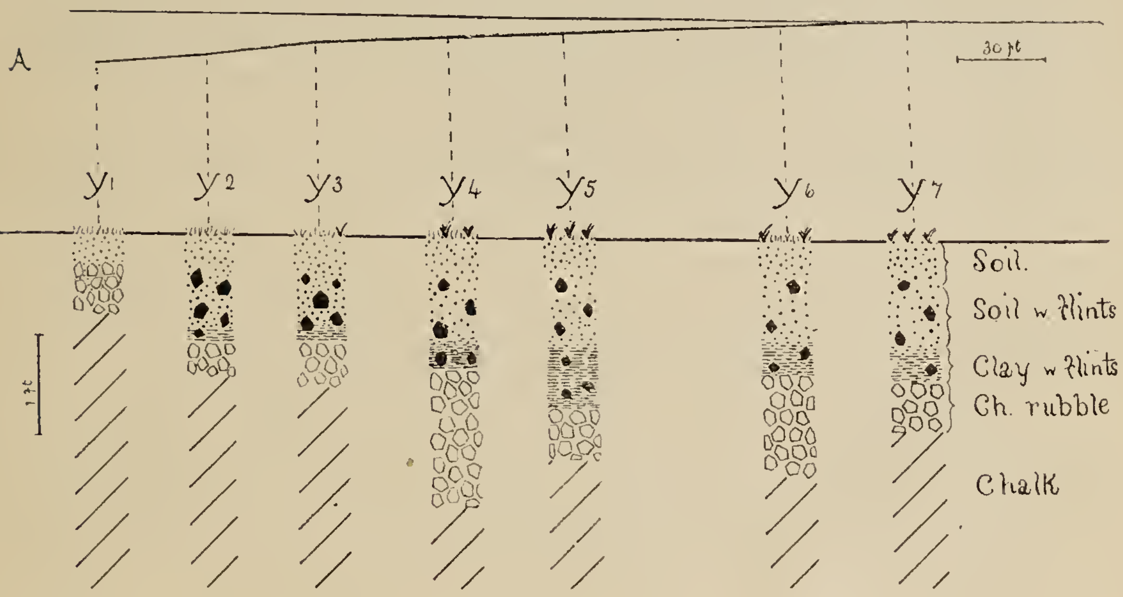


Fig. 2. Section from holes Y_1 to Y_7 on mapped area (Fig. 1) showing the thickness and distribution of soil and deposits overlying the chalk. The section A shows the actual slope of the ground along the line of holes plotted on a smaller scale.

Y_5. *Thick heather.* Top ¼-inch of soil rather darker in colour, but no peat formed. Layer of stiff yellowish clay-with-flints over irregular surface of chalk rubble 18 inches from surface. Chalk at 24 inches. General effect is that of good deep, rather heavy loam resting on thin layer of clay-with-flints over chalk. Soil retentive after rain. Soil A taken from here.

Y_6. *Grass patch surrounded on three sides by heather.* Similar to Y_5. Chalk at 24 inches. Chalk rubble at 15 inches. Soil retentive in wet weather. Soil B taken from here.

Y_7. *Thick heather.* Similar to Y_5. Very large unworn flints present. Chalk at 22 inches. Chalk rubble at 16 inches. *Calluna* rooting down into chalk rubble.

Y_8. *Edge of heather area.* Similar to Y_7. Chalk at 24—28 inches. Chalk rubble at 16—20 inches. Scattered patches of *Calluna.*

Y_9. Outside heather area, but latter shews a tendency to spread in this direction. Ground levels suggest that the clay-with-flints continues for some distance in this direction. Chalk rubble at 17—18 inches from surface.

I. Reference to the details obtained from the holes and sections plotted from them (Fig. 2) shows that the solid chalk occurs at a depth below the surface varying from 9 inches at Y_1 to over 2 feet 6 inches in the middle of the heather area.

The thickness of chalk rubble above is variable and its upper limit is very irregular. In the hole Y_3 for instance, the top of the rubble comes within 8 inches of the surface at one point, within 16 inches at another. The overlying deposit of clay-with-flints is

TABLE I.

		Y_1	Y_3	Y_5	Y_6	Y_7	Y_9
6 inches	Nature of soil.	Chalky	Loam	Loam	Heavy Loam	Heavy Loam	Heavy Loam
	Percentage of $CaCO_3$	*43·6	·005	·193	·009	·064	·016
12 inches	Nature of soil.	—	Heavy Loam	—	Clay	Clay	Clay
	Percentage of $CaCO_3$	—	2·44	—	·014	—	—

* This sample was taken at 3 inches instead of 6 inches owing to the thinness of the soil.

		X_2	X_3	X_4	X_5	X_6
6 inches	Nature of soil	Clayey Loam	Heavy Loam	Clay	Heavy Loam	Loam.
	Percentage of $CaCO_3$	3·38	·732	·123	·027	·093
12 inches	Nature of soil	—	—	Heavy Clay	—	—
	Percentage of $CaCO_3$	—	—	·024	—	—

thickest towards the middle of the heather and thins out towards Y_1, being practically absent at Y_2, where solid chalk occurs 1 foot 4 inches below the surface. The distribution of the heather on this side appears to be determined by the depth of clay-with-flints present, but at Y_7, where *Calluna* is very thick and quite 2 feet high, the plants were rooting down into the chalk rubble 16 inches below the surface, and penetrating lumps of chalk. These roots appear to be functional and healthy and contain *mycorhiza*.

Section X shewed a similar distribution of the clay-with-flints, thickest in the heather area and thinning out on the slope of the down towards the N.W.

Table I shows the nature of the soil and the percentage of calcium carbonate present in the soils from some of the holes at depths of 6 inches and 12 inches respectively.

The percentage of calcium carbonate present is very low all over the heather area. Although this is the case and the spread of *Calluna* appears to be definitely related to the distribution of the clay-with-flints over the chalk, small lumps of the latter occur within the rooting area.

The root system of the heather is contained chiefly within the first 12 inches of soil, but as noted above, in some of the holes, roots were growing into the chalk rubble and were apparently functional.

Calluna is recorded from limestone soils in various part of Great Britain and Ireland, although it is well to remember that a soil on limestone is not necessarily rich in calcium carbonate unless the rock is near the surface.

Taking into account the somewhat conflicting horticultural evidence, which records species of *Erica* usually regarded as calcifuge, and also *Dianthus alpinus*, as growing well on certain limestones, although refusing to do so on chalk, and also Graebner's explanation of the behaviour of calcifuge plants towards lime, the present work seems to favour the view that factors other than the percentage of $CaCO_3$ present are involved in the soil preferences shown by so-called " lime-shy " plants like *Calluna*, although it does not support the conclusion that *Calluna* cannot compete successfully on soils containing a high proportion of soluble mineral matter.

II. A preliminary analysis indicated a relatively high proportion of magnesia in the soil in which the heather was growing. As it was thought this might possibly have some significance in regard to the distribution, detailed analyses were made of the soils from four stations.

A. Soil from heather area near Y_5.

B. Soil from grass patch in heather near Y_6.

C. Thin soil over chalk near Y_1.

D. Soil over clay-with-flints outside the heather area.

For comparison with the above, three typical soils have been chosen.

E. Soil from a chalk down in Dorset. F. Stiff arable loam from Milbourne, Dorset, on clay-with-flints, and G a poor soil on the Bagshot Sand from Broadstone Heath, Dorset, on which *Calluna* is naturally abundant.

The detailed analyses, mechanical and chemical, of these soils are given in the following Table.

TABLE II.

	Berkshire and Wiltshire Downs.				Dorset.		
Station.	A	B	C	D	E	F	G
Nature of Situation.	Heather Area.	Grass in Heather.	Soil over Chalk.	Loam and Flints.	Chalk Down.	Stiff. Loam.	Waste Common.
Locality.	Botley.	Botley.	Botley.	Botley.	Cerne Abbas.	Mil-bourne.	Broad-stone Heath.
Geological Formation.	Clay with Flints.	Clay with Flints.	Upper Chalk.	Clay with Flints.	Upper Chalk.	Clay with Flints.	Bagshot Sands.

A.—Mechanical Analysis of 100 parts of air-dry soil.

Stones more than ½" dia.	27·4	20·6	11·2	·9	9·0	7·0	11·0
" " " 1/10" "	15·2	5·2	2·0	1·5	—	—	—
Chalk	·1	—	31·3	—	—	—	—
Fine Earth, less than 1/10"	57·3	74·2	55·5	97·6	91·0	93·0	89·0

B.—Mechanical Analysis of 100 parts of air-dry fine earth.

Moisture	3·97	5·41	4·15	4·71	2·0	3·0	1·2
Organic Matter	12·57	13·92	18·42	12·16	9·1	7·9	6·3
Calcium Carbonate ...	—	—	41·80	—	54·0	·36	·05
Fine Gravel, 3-1 *mm.* ...	1·65	1·46	1·30	·84			
Coarse Sand, ·12 *mm.*	2·90	1·90	1·38	2·80	18·0	60·0	81·5
Sand, ·2-·05 "	22·80	23·50	5·67	27·40			
Silt, ·05-·01 "	33·90	30·75	12·31	34·70	7·9	17·1	4·5
Fine Silt, ·01-·005 "	14·25	13·95	5·75	11·44			
Clay	7·55	8·60	5·67	4·67	9·0	12·0	6·5
Loss on Solution ...	·41	·51	3·55	1·28			

C.—Chemical Analysis of 100 parts of air-dry fine earth.

Moisture	3·97	5·41	4·15	4·71	2·0	3·0	1·2
Organic Matter	12·57	13·92	18·42	12·16	9·1	7·9	6·3
Nitrogen	·345	·358	·547	·369	·19	·16	·16
Insoluble Mineral Matter	70·50	67·80	26·28	72·00	23·40	75·70	89·50
Constituents soluble in strong acid	12·96	12·87	51·15	11·13	65·50	13·40	3·00
Phosphoric Acid, P_2O_5	·40	·29	·23	·45	·36	·44	·20
Sulphuric Acid, SO_3 ...	·13	·18	·27	·13	·29	·32	·24
Potash, K_2O	·17	·21	·13	·22	·38	·17	·18
Soda, Na_2O	·15	·18	·16	·19	·12	·29	·54
Magnesia, MgO	·55	·57	·58	·33	·27	·41	·17
Calcium Carbonate, $CaCO_3$	—	—	41·80	—	54·00	·36	·05
Lime other than this as Calcium Oxide, CaO	·70	·68	·90	·31	5·40	·70	·77
Iron Oxide, Fe_2O_3 ...	4·07	3·91	2·40	3·48	1·70	5·43	·55
Alumina, Al_2O_3 ...	7·27	7·34	4·43	6·21	2·89	5·31	·31
Constituents soluble in 1% Citric Acid.	—	—	—	—	—	—	—
Phosphoric Acid, P_2O_5	·018	·017	·007	·047	·020	·015	—
Potash, K_2O	·009	·005	·023	·009	·009	·011	—
Reaction	Neutral.	Neutral.	Slightly Alkaline.	Neutral.	Alkaline.	Neutral.	Acid.

Comparison of these figures brings out the following points:

1. The mechanical composition of the soils A, B, and D is very similar to that of a good average fertile loam. The hygroscopic water held by all is rather high, especially in the case of B, and examination of the soils, *in situ*, during the progress of the work in damp weather showed that A, B and D were retentive of water as compared with C, and were rather more sticky in texture.

The stickiness is possibly due in part to the excess of magnesia over the carbonate of lime present as well as to the deficit of lime (9). Soil A under *Calluna* contrasts sharply as regards physical character with G—a soil from a *Calluna*-heath.

2. In chemical composition A, B, and D are very similar. The total amount of soluble mineral matter is high; the figures for phosphoric acid and nitrogen are higher than those in F; the soluble mineral matter is very much higher than that in G which is typical of dry sandy heath soils on the Bagshot Beds where *Calluna* is a prominent feature of the vegetation. These facts do not appear to agree with the conclusions of Graebner (loc. cit.) and others, as to the improbability of *Calluna* competing successfully with other plants on good soils.

A striking feature is the high proportion of magnesia to calcium carbonate in the soils from the mapped area, the latter being indeterminable in amount in A, B, and D on clay-with-flints. It is perhaps worth noting in this connexion that the amount of magnesia in D where *Calluna* does not occur, is considerably lower.

All the clay-with-flints soils (A, B, and D) give a neutral reaction, a feature of some interest in view of the fact that soils bearing *Calluna* are usually acid (*e.g.*, Soil G). The two down soils C and E are slightly alkaline.

III. With regard to the existence of an edaphic factor, comparative chemical analyses do not throw much light on the problem, except in so far as they confirm the view that the heather soil is a fertile one, relatively rich in available mineral constituents; the high proportion of magnesia is the only striking feature in the Botley soils. This is not peculiar to the soil on which the heather is growing, but is a feature common to the three soils A, B, C, and in a less degree to D on clay-with-flints outside the *Calluna* area. Comparison with the figures for E shows that while the absolute amount of magnesia present in the latter is not much less, the ratio of magnesia to calcium carbonate is strikingly different and is in excess of that usually found in fertile soils.

A high percentage of magnesia seems to be a characteristic feature of soils on the clay-with-flints. Analyses of these soils occurring in Kent and Surrey as given in the recently published Board of Agriculture Report (10) show also a high percentage of magnesia, although in all the cases given, the proportion of $CaCO_3$ is much higher than in the Botley soils. This is due to the fact that most of these soils are under cultivation and have been artificially limed. Three of the natural soils, unlimed, also show a higher percentage of $CaCO_3$ as compared with magnesia than do those on Botley Down, *viz* :—

MgO	·3	·22	·38
Carbonates as $CaCO_3$	·02	·07	·06

The effect of liming is well shown in the case of two adjoining fields, one of which has a very low percentage of carbonates (·08 in the subsoil), the other has been artificially limed. The former is reputed the stiffest soil in the district, and has been laid down to grass, the latter yields good crops. The improvement due to liming is attributed, no doubt justly, to the improvement in texture induced in the soil. The possibility of it being in part due to the altered relations between magnesia and calcium carbonate, as suggested by the Woburn experiments noted below, does not appear to be eliminated, although it is only fair to add that in the same report a few fertile soils are recorded from other districts with a comparatively high proportion of magnesia.

Sufficient data, however, are not available at present to warrant any definite suggestion as to the significance of the decreased amount of magnesia in D from which *Calluna* is entirely absent.

Experiments dealing with the proportional amounts of magnesia and calcium carbonate in the soil have been recently carried out on wheat and barley at the Woburn Experimental Station (9). The earliest experiments were made on pot plants and were followed by field experiments with similar results.

Starting with a soil containing magnesia and calcium carbonate in the proportion of 1 : 2, it was found that as the magnesia was increased so the inferiority of the crop became more marked. Vegetative peculiarities were noticed, such as the development of an abnormally extensive and fibrous root-system, the soil became darker in colour, and rather more sticky and retentive of water. These results have not been confirmed by other observers up to the present.

The observations of Loew (11) on the physiological rôle of calcium and magnesium salts in plants are also of interest in this connexion. Recent papers by Konowalow (12) and Lemmermann (13) are not in agreement with Loew's conclusions nor with the results of the Woburn experiments.

Konowalow working with sand and water cultures, is of the opinion that observed differences in growth must be attributed to varying concentrations of the solutions.

Lemmermann concludes from field experiments on various crops, that the ratio of CaO: MgO may be altered within wide limits without appreciably affecting the crop. He finds, however, that dressings with lime and magnesia affect absorption of phosphoric acid, in the direction of increased phosphoric acid absorption with increased proportion of magnesia.

He finds also that the micro-organisms of the soil were unaffected by changes in the Ca0 : Mg0 ratio.

Our experiments during the past year with *Calluna* in artificial cultures and in pot cultures of the Botley soils, suggest that a soil factor is present which affects the germination of the two seeds and also the subsequent growth of the seedlngs. They are inconclusive at present as to the significance of magnesia in this connection.

Since relations with the soil are peculiar in *Calluna* and in other Ericaceæ, owing to the presence of mycorhiza, it seems possible that a clue is to be sought for in the biological rather than in the chemical or physical peculiarities in the soil.

SUMMARY.

Calluna vulgaris occurs in various places on the chalk downs of the South of England. The data hitherto recorded make it difficult to account for the existence of isolated and often sharply defined *Calluna* communities in these situations, such communities being apparently invasions and occurring on areas distinguished by the presence of heavy loamy soil, rich in mineral constituents although poor in lime.

Although the thickness of the overlying deposits, and consequently the amount of calcium carbonate present in the rooting medium apparently determine the distribution of the *Calluna*, functional roots were found in places growing into the chalk rubble, and small lumps of chalk occur occasionally within the rooting area.

The soil on which *Calluna* is growing contains a relatively high proportion of magnesia. It is suggested that this may be of significance either chemically, or in so far as it affects the physical or biological conditions of the soil, but until the results of experimental work are available, no definite conclusion can be arrived at. With this exception no evident edaphic factor has as yet been found to account for the successful competition of the heather. The soil is neutral in reaction.

Calluna is associated with several species alien to the surrounding vegetation. These, as well as the flora of the neighbouring chalk down and of the clay-with-flints are being recorded.

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THE STRUCTURE OF THE CELL-WALL AND THE APICAL GROWTH IN THE GENUS *TRENTEPOHLIA.*

By G. S. West, M.A., D.Sc., F.L.S.,
and
Olive E. Hood, M.Sc.

[With Figs. 1—6.]

THE remarkable structure of the cell-wall of *Trentepohlia Montis-Tabulæ* var. *ceylanica*, which was very briefly commented upon at the time that variety was described,[1] has since led to a detailed examination of the cell-wall of this and other members of the genus.

The structure of the cell-wall and the growth of the apical cell in this species from Ceylon are first dealt with, after which briefer statements on the structure of the wall in other species are given for comparison.

Trentepohlia Montis-Tabulæ (Reinsch) De Toni var. Ceylanica, W. & G. S. West.

This is a large *Trentepohlia* with a thicker cell-wall than occurs in any other known member of the genus. The cells are 52—57μ in length, 19—34μ in breadth, and the cell-wall attains a thickness of 7·5 (or even 8) μ. It is distinctly lamellose, exhibiting a peculiar and characteristic oblique surface striation. De Toni[2] describes the walls of the type-form as "thick and lamellose, with very delicate, decussating striations."

In surface view the wall has the appearance of a network of interlacing fibres, but in optical section it is seen to consist of somewhat oblique lamellæ, all of which are slightly divergent upwards. This structure is rendered more evident if the filaments are cleared and caused to swell, which can be done in a most satisfactory way either by the use of concentrated sulphuric acid or an ammoniacal solution of cupric hydrate. Under this treatment the lamellæ gradually swell up and separate, giving the plume-like appearance represented in Fig. 1. A similar swelling can also be brought about by treatment with concentrated potash solution.

The transverse walls are also lamellose, the lamellæ being continuous with those of the lateral walls. The form of the transverse

[1] W. & G. S. West in Trans. Linn. Soc., bot. ser. 2, 1902, p. 131.

[2] De Toni, Syll. Alg., 1889, p. 240.

wall is a little variable, but in most cases the central part is shaped like a watch-glass with the convex side usually towards the apex of the filament. When the cells are swollen they frequently split apart by the rapid breaking down of the transverse walls.

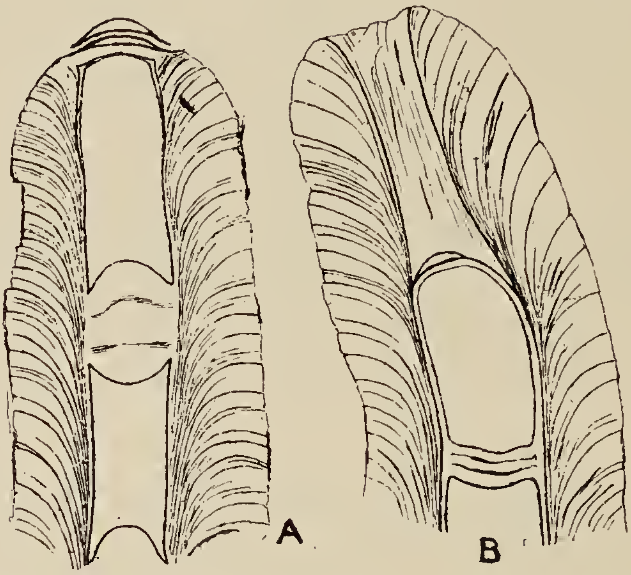

Fig. 1. Ends of two branches of *Trentepohlia Montis-Tabulæ* var. *ceylanica* treated with an ammoniacal solution of cupric hydrate. This structure can only be seen for a brief period after which the lamellæ are gradually dissolved. In B the apical cell had been damaged and its functions taken on by the penultimate cell, which had already developed an apical cap. A and B, × 500.

Thus, the statement of Brandt[1] that the transverse walls are simple is not true of all the members of this genus. The lamellæ of the transverse walls, like those of the longitudinal walls, consist entirely of cellulose. This is clearly shown by the reactions of the cell-walls to reagents and stains. They are soluble in an ammoniacal solution of cupric hydrate after first taking on a blue colouration, and also soluble in concentrated sulphuric acid. With a potash solution they swell considerably. Sulphuric acid and iodine solution give a deep blue colouration, and with chlor-zinc-iodine the filaments assume a deep violet colour. The walls also stain with methylene blue, safranin, rosanilin-violet, eosin and a watery solution of fuchsin.

The apical cell.—Growth in the genus *Trentepohlia* is entirely apical, and the wall of the apical cell in *T. Montis-Tabulæ* var. *ceylanica* consists of successive thin lamellæ, which are upwardly and outwardly divergent. The lamellæ are not entirely continuous round the cell, but each lamella is laid down only within the upper half or upper two-thirds of the cylindrical side walls and across the apex itself. As the growth of the apical cell continues the last-deposited lamella increases in superficial area and gradually bursts through the previous layer which covered the apex, so that the cell-wall at the extreme apex has but one thin layer of cellulose and a curious apical cap. This process is continually going on as the apical cell grows in length, and the structure of the cell-wall can be seen by reference to Fig. 2.

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[1] F. Brandt in Beihefte zu Botan. Centralbl. XII., 1902.

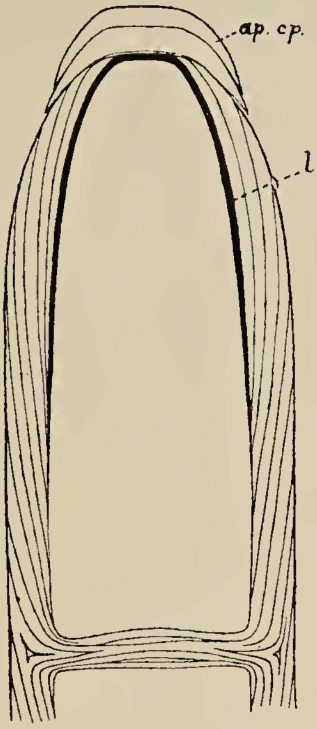

Fig. 2. Semidiagrammatic figure of the structure of the wall of the apical cell of *T. Montis-Tabulæ* var. *ceylanica*. The innermost layer of cellulose (*l*) is filled in black. *ap. cp.*, apical cap.

The *apical cap* fits firmly over the end of the cell, covering the delicate end-wall. It is a secretion of the apical cell, and can be seen in all stages of growth, the first indication of its formation being quite evident at the apex of even the youngest branches. The newly formed cap is homogeneous, consisting of one layer of substance, but older caps may consist of two or more layers, which in many cases become partially free. Thus, the free end of a cell is sometimes surmounted by a successive series of apical caps (Figs. 3 and 4). Occasionally the caps appear to be raised on a short pedestal of the same substance.

When removed, the cap is seen to be hat-shaped or bonnet-shaped, thick in the flattened middle portion and rapidly thinning down to a fine, deeply serrated fringe at the downwardly turned edges (Fig. 4 C). This fringe surrounds the apex of the cell and fits very closely over the terminal portion of the thick side-walls, thus keeping the cap in position.

Injury or removal of this cap appears to be followed by the rapid formation of another one.

The apical cap differs from the cell-wall in structure and in its behaviour when treated with various reagents and stains. The caps are insoluble in an ammoniacal solution of cupric hydrate, although they may swell considerably, and they are very slowly soluble in sulphuric acid. They are not coloured with sulphuric acid and iodine, neither are they stained with chlor-zinc-iodine. These negative reactions indicate that the caps are either chitinous or pectic in character. Further tests showed no staining with picro-carmine or picric acid and borax-carmine, nor any yellow colouration with picric acid or picro-sulphuric acid. Moreover, they are easily soluble in a 2% solution of potash, and therefore the caps do not contain chitin. They stain deeply, however, with methylene blue,

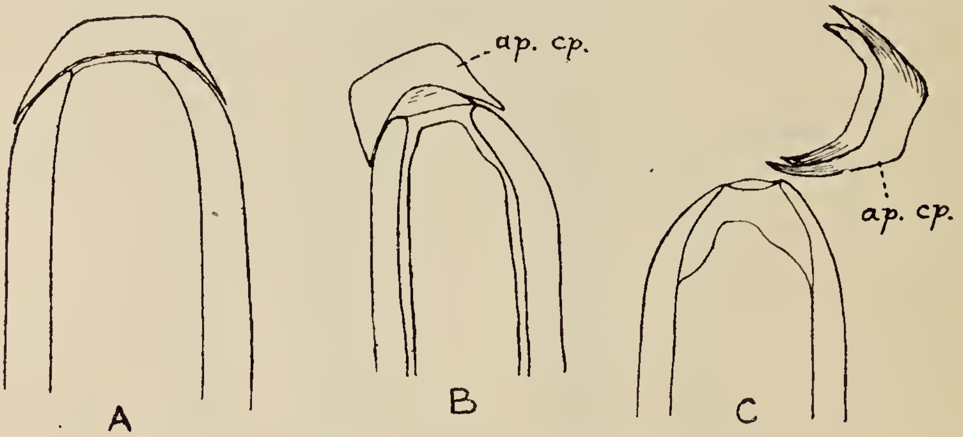

Fig. 3. Three apical cells of *T. Montis-Tabulæ* var. *ceylanica* showing the apical caps. In C there are two caps both of which have come loose on treatment with chloral hydrate. × 800.

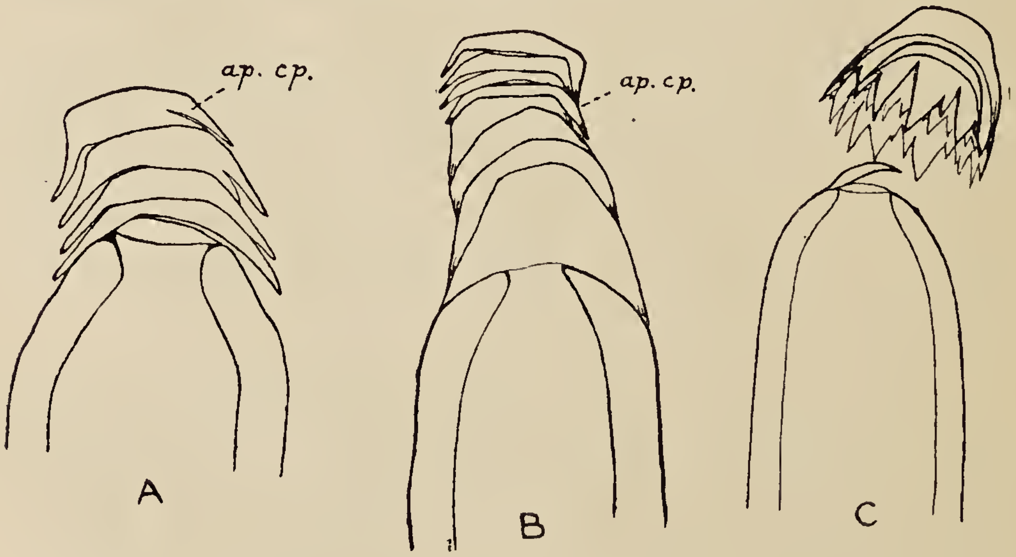

Fig. 4. Three apical cells showing a series of apical caps. In C the serrated fringe of a loose cap is well shown. × 800.

Bismarck brown, and fuchsin, and one must therefore conclude that *the caps consist entirely of pectose.*

Brandt[1] has stated that the apical caps which are so frequently developed at the extremity of a branch consist of cellulose, and that they are the remains of dead, terminal zoogonidangia. As regards the species under examination, both of these statements are erroneous. In the first place, the caps do not consist of cellulose, and secondly, they are without doubt secreted by the apical cell, and at no time have any connection with dead zoogonidangia. We invariably find in the case of an empty terminal zoogonidangium that the supporting cell takes on the function of an apical cell, and far from carrying the remains of the zoogonidangium at its extremity actually grows through it, leaving it behind as a sort of collar.

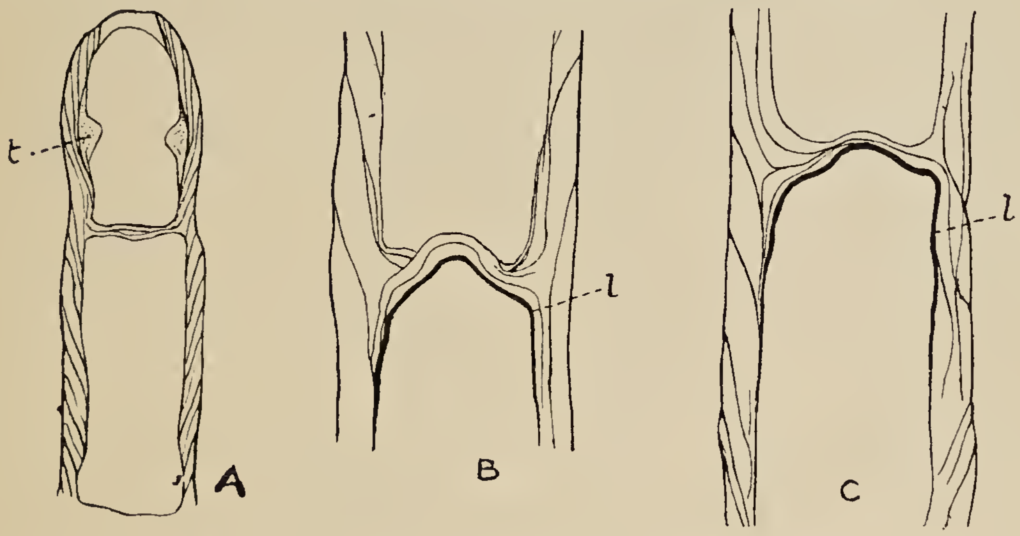

Fig. 5. A, apex of branch (seen in optical section) of *T. Montis-Tabulæ* var. *ceylanica* showing the beginning of new transverse wall (*t*). B and C, showing the completed transverse wall between the apical and penultimate cells; *l*, a layer of cellulose added after the completion of this wall. A, × 500; B and C, × 800.

In the division of the apical cell the transverse wall arises as an annular ingrowth from the middle region of the lateral walls (Fig. 5 A). The ingrowth in its early stages is at right angles to the longitudinal walls, but towards its completion it usually bends upwards so that the last-formed part of the transverse wall is convex towards the free end of the apical cell. The transverse wall is stratified and as the wall is completed the corresponding lamellæ fuse.

Soon after the formation of the new transverse wall, another layer of cellulose is frequently added within the upper half of the penultimate cell (Fig. 5 B and C, *l*).

[1] Brandt, l.c.

OTHER SPECIES OF TRENTEPOHLIA EXAMINED.

Trentepohlia aurea (L.) Mart. Both living and fixed material of this species were examined. The cell-wall is lamellose, the lamellæ showing up clearly on treatment with strong sulphuric acid. The latter are less divergent than those of *T. Montis-Tabulæ* var. *ceylanica*, and each newly-formed lamella extends proportionately further down the lateral walls. The extreme apex of the wall also consists of several lamellæ and is much thicker and stronger than in *T. Montis-Tabulæ* var. *ceylanica*. Only the older lamellæ are broken through in the growth of the apical cell, several of the newer layers increasing in area at the same time. This is very similar to the mode of growth described by Schmitz[1] and also by Strasburger[2] in the marine alga *Bornetia secundiflora*.

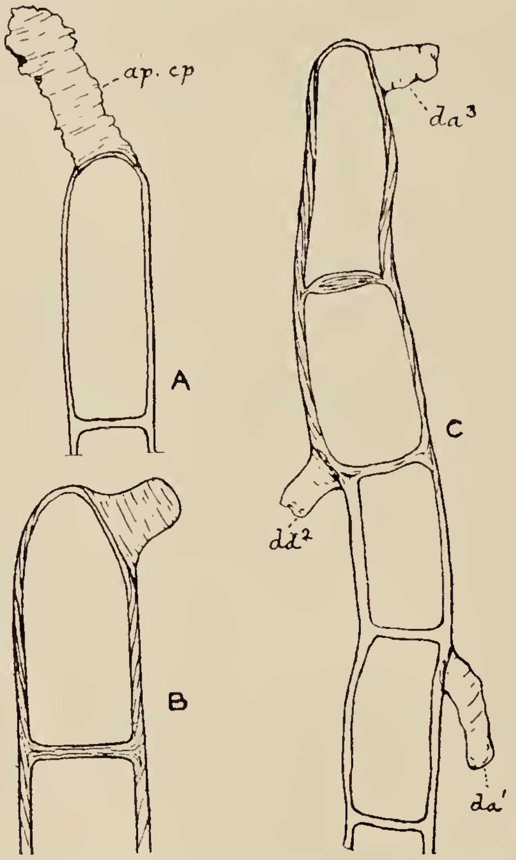

Fig. 6. Apices of three filaments of *T. aurea*. × 800. A, shows a very irregular and much elongated apical cap. B, apical cell with a laterally displaced apical cap. C, end of filament showing three successively displaced apical caps (*da*¹, *da*², *da*³).

The cell-wall consists entirely of cellulose.

The apical secretions of pectose are again present, but they are not the bonnet-shaped caps previously described. They do not fit like an inverted bowl over the end of the cell, but often project from the extreme apex as an irregularly cylindrical stump. They often appear to grow for some time, and may attain a length of 40μ. (Fig. 6A).

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[1] Schmitz, "Bildung und Wachstum der pflanzlichen Zellmembran," Sitzungsber. der neiderrhein. Ges. für Natur. u. Heilkunde zu Bonn, 1880.

[2] Strasburger, "Ueber Bau und Wachstum der Zellhäute," Jena, 1882, p. 189.

During the growth of the apical cell the osmotic pressure is considerable. The weakest part of the wall is the apical part immediately below the apical secretion of pectose, and normally this is the region of the cell-wall in which the successive cellulose lamellæ become distended and gradually broken through. It happens frequently, however, that the weakest portion of the wall, and therefore the line of least resistance, becomes shifted laterally to some point below the apex, under which circumstances this point soon becomes apical in position and the former apex lateral. In this way an apical cap often becomes lateral, and as the apical cell grows it is left some distance behind the growing apex. If, on the division of the apical cell, the next transverse wall is above the place of attachment of the cap, the latter will be on the penultimate cell. During this time a new apical cap is formed, and a repetition of the process frequently results in filaments with several lateral excrescences, each of which was at one time an apical cap (Fig. 6C). Reagents and stains show that all these caps consist entirely of pectose.

T. aurea var. *lanosa* Kütz. In this variety the branches taper so that the apical cells are much narrower. The cell-walls are lamellose with more divergent lamellæ. Apical caps narrow and not so well developed as in *T. aurea* type.

T. abietina (Flot.) Hansg. In this smaller species the cell-walls are lamellose with divergent lamellæ. The wall at the extreme tip of the apical cell is fairly thick and apical caps are developed only to a small extent.

T. odorata (Ag.) Wittr. The lamellæ of the cell-walls are almost parallel to the long axis and for the most part extend round the apex of the apical cell. The apical caps, when present, are minute and rudimentary, and were only discerned by staining.

T. villosa (Kütz.) De Toni. The lamellæ of the cell-walls are almost parallel. Rudimentary apical caps of minute size were sometimes present as in the preceding species.

T. polycarpa Nees et Mont. The lamellæ of the cell-walls are almost parallel. Extreme tip of apical cell relatively thin, with a thin apical cap only definitely evident on staining with chlor-zinc-iodine.

T. phyllophila W. & G. S. West. The lamellæ of the cell-walls are practically parallel, and for the most part extend round the free end of the apical cell. Apical caps not discovered.

T. calamicola (Zeller) De Toni. No definite results were obtained by the examination of this species, the specimens of which were preserved in alcohol. The whole exterior of filaments and branches appeared to be encased in a thin sheath of brown substance which entirely resisted the action of reagents, even of concentrated sulphuric acid. Both filaments and branches are frequently united into a sort of meshwork by this resistant substance. (A similar outer covering of resistant material was also present in a larger, but undetermined, species from Ceylon).

SUMMARY.

In the genus *Trentepohlia* the cell-walls are lamellose and the lamellæ consist of cellulose.

In some species the lamellæ are approximately parallel, and the growth of the apical cell takes place by the proportionate distention and permanent increase in area of all these layers.

In other species the lamellæ diverge upwardly and outwardly, and the growth of the apical cell takes place by the distention of only the newly-formed layers, the older layers being burst through.

In one species (*T. Montis-Tabulæ* var. *ceylanica*) the extreme case is reached where all the layers of the cell-wall are burst through at the apex by the extension of the last-formed lamella.

In many species of the genus, apical caps of pectose are secreted at the free end of the apical cell. These caps vary in the extent of their development. They are for the most part absent in species in which the lamellæ of the cell-wall are parallel, and in which the wall at the free extremity of the apical cell is of approximately the same thickness as the rest of the cell-wall. They are, however, developed in a varying degree in those species in which the lamellæ of the cell-walls are divergent. The fewer the lamellæ at the growing extremity of the apical cell and the more complete is the development of the apical cap.

Species of *Trentepohlia* grow only in a damp atmosphere, and the structure of the apical cell in many species is such that its thin extremity requires efficient protection during those periods when the humidity of the atmosphere is below the normal. This protection is afforded by the apical cap, which may therefore be regarded as protective in function.

In some species (e.g., *T. aurea*) the apical cap may become cumbrous and act rather as an impediment to growth than otherwise, in which case it is frequently displaced by a slight change in the direction of growth of the apical cell, and a new cap developed.

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THE ANATOMY OF THE MUMMY PEA.

BY R. H. COMPTON.

[WITH FOUR FIGURES IN THE TEXT.]

THE Mummy Pea is a striking variety of *Pisum sativum* characterised by the production, in the upper part of the plant, of a greatly dilated axis bearing a dense cluster of leaves and short inflorescences arranged promiscuously.[1] The broadening begins to take place about a foot above the ground, and the plant produces no long lateral branches. The whole appearance is abnormal, and is evidently the result of a fasciation. As will be shewn in the sequel the structure is that of the very rare condition known as ring-fasciation. The Mummy Pea breeds perfectly true, and its peculiar character behaves as a simple recessive in crosses with the normal type.[2] Owing to the distinct appearance and its power of breeding true it has sometimes been considered as a distinct species, *P. umbellatum*, Miller.

A closer inspection shews that the distended part of the main axis is funnel-shaped: its tip is open, and a probe can be passed through the aperture into the body of the plant. Thus the whole of the cavity of the dilated stem is open to the external air, insects and débris being able to enter freely.

An investigation of the anatomy of the axis reveals a very curious condition. The lowest internodes exhibit the normal structure of the Vicieæ, with "medullary" xylem and extra-stelar stipular bundles: higher up this gives place to the development of a fistular pith and a single ring of collateral vascular bundles. In the uppermost region of the swollen funnel-shaped axis, however, two continuous concentric rings of vascular tissue are present. The outer of these rings is directly continuous with the single ring of bundles below, and the different vascular elements of xylem, phloem, etc., have the normal orientation. The inner ring, on the

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[1] A photograph is given by A. D. Darbishire ; "Breeding and the Mendelian Discovery," 1911, Fig. 8.

[2] G. J. Mendel. Verh. naturf. Ver. in Brünn, Abh. IV., 1865 (Engl. Transl. by W. Bateson, "Mendel's Principles, etc," 1909, p. 317).

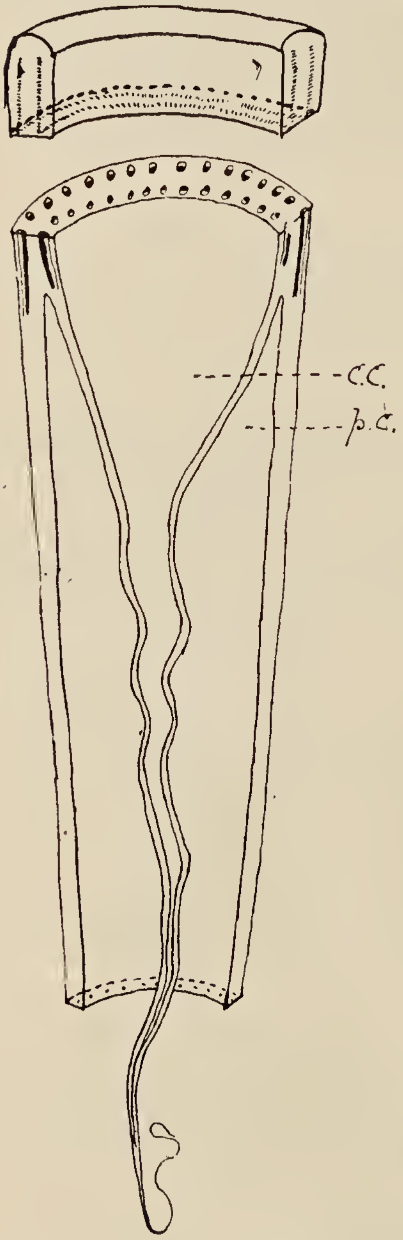

Fig. 1. Diagram of the fasciated portion of the stem, as seen if split longitudinally: above, a scheme of half the annular apical meristem. (In the bundles xylem is black, phloem left clear. *c.c.*= central cavity of the funnel; *p.c.* = lysigenous cavity equivalent to the fistular pith).

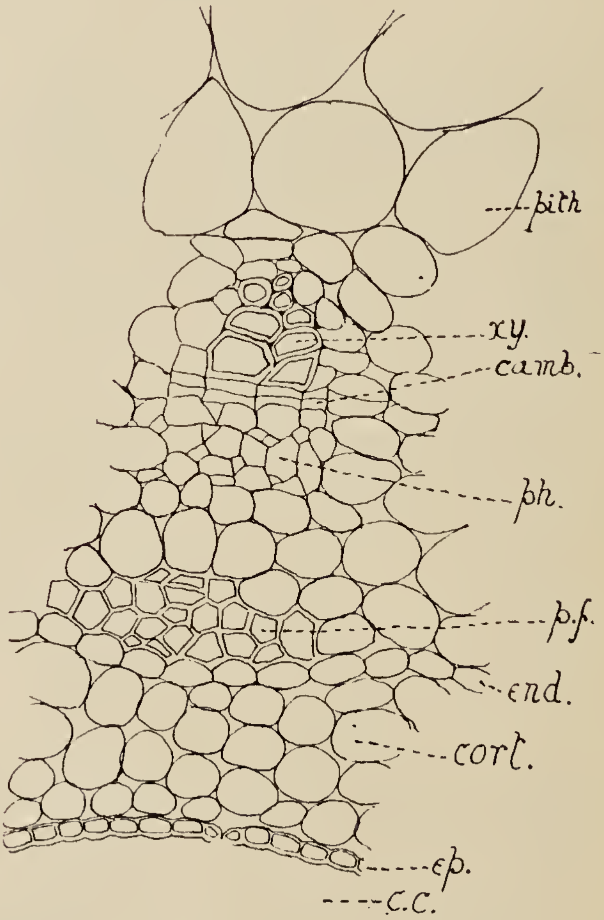

Fig. 2. T.S. of a bundle of the internal system. (*ep.* = internal epidermis, with stoma; *cort* = cortex; *end* = endodermis; *p.f.* = pericycle fibres; *ph.* = phloem; *camb.* = cambium; *xy.* = xylem).

other hand, has an inverse orientation of tissues: the xylem lies towards the exterior, and cambium, phloem, pericycle and endodermis lie successively nearer the geometrical centre of the axis. Moreover, within the endodermis are found a few layers of parenchymatous cells resembling a cortex, containing chlorophyll and interpenetrated by air spaces; and these are bounded on the inside by a well-defined epidermis with cuticle and numerous perfect stomata, this internal epidermis surrounding the large central air cavity (Figs. 1, 2, 3).

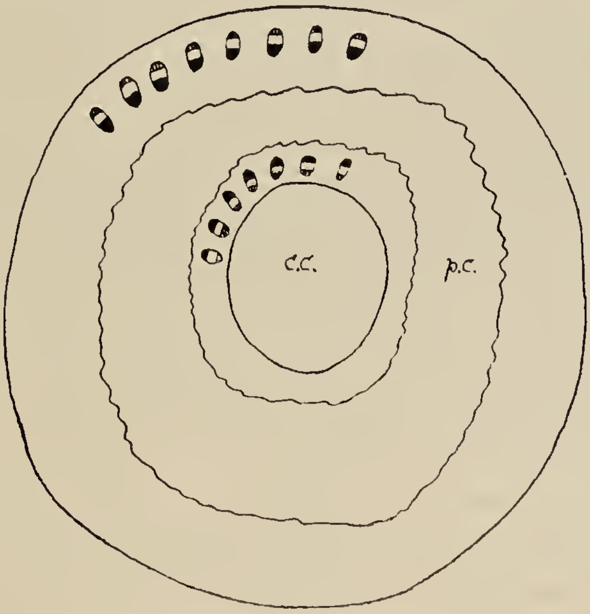

Fig. 3. Diagram of a T.S. of the whole axis at the level of "*p.c.*" in Fig. 1. (Xylem black, phloem clear, pericycle fibres shaded).

In between the two rings of vascular bundles is found a zone of parenchymatous tissue, histologically like a medulla; and like the pith in the normal stem this tissue becomes fistular when beyond a certain age. The result is that the two rings of vascular and other tissues become separated in the mature state by a cylindrical lacuna bounded by torn medullary cells (Fig. 3). If the stem be cut open in the lower part of the dilated region the internal ring of tissues can be seen hanging freely within this lysigenous space, or attached only at the slender thread-like tip[1] (Fig. 1). The internal cylinder is usually somewhat coiled and twisted: it terminates below in the region of a leaf-node. No vascular connection was discovered between the bundles of the outer cylinder and those of the inner, either at the node at which the latter takes its origin, or at any point of its course. The leaves and branches connect only with the outer ring of bundles. In a somewhat similar case described by Nestler[1] in *Veronica longifolia*, and also in the example of a tubular spadix of *Peperomia maculosa* described by de Vries,[2] the internal surface of the funnel also gave off leaves and even flowers: but in the Mummy Pea no such structures have been observed. Further, in the case described by de Vries, the internal inversely oriented bundles are continuous with the medullary bundles normally found in the Piperaceæ, the connection being effected through a rotation of individual bundles.[3] In the Mummy Pea, however, the inner ring of bundles is quite independent of the outer, and is not connected by means of vascular tissues with the root system on the one hand, nor with the leaves and branches on the other. Under these circumstances it is perhaps surprising to find that the inner ring of bundles shews as complex an organisation as the outer "normal" ring (Fig. 2). All the usual tissues are present, the only difference being that the actual bulk of each tissue in each bundle is rather less than in a bundle of the outer ring.

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[1] It was the curious appearance of this internal cylinder that attracted the attention of Miss E. L. Stephens, to whom I am indebted for the suggestion of an anatomical study of the structure. The appearance is in some respects like that encountered in certain cases where medullary bundles are present and where these persist as isolated cords after the embedding pith has been ruptured. Mr. Shrubbs of the Cambridge Botany School kindly gave me a petiole of *Heracleum giganteum* shewing one such cord originating in a nodal diaphragm, and containing a single collateral vascular bundle. This phenomenon is, however, of a different kind from that here described in the Mummy Pea.

The central cavity of the funnel-like stem contains air and is bounded by an epidermis. The histological structure of this internal epidermis is very different from that of the external. Whereas the latter consists of narrow cells much elongated longitudinally and only seldom pierced by stomata, the internal epidermis is composed of much broader and less elongated cells, very thinly cuticularised and penetrated by a great number of stomata. The tissues abutting on the epidermis in each case are fairly similar: the inner cortex contains a considerable amount of chlorophyll, though not so much as the outer.

It would thus appear that the whole internal complex of tissues, assimilatory, protective and conducting, functions in a large measure independently of the rest of the plant: any interchange of water and food-stuffs between the outer and the inner systems must take place through parenchymatous and not specifically conducting cells. In any case the internal system of tissues can have little importance in furthering the development of leaves, flowers and fruit: and it is probable that its existence is the expression of some morphological determination rather than of the need of subserving a physiological function in relation to the whole plant.

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[1] A. Nestler "Ueber Ringfasciationen" Sitzungsb. d. k. Akad. d. Wiss. Wien (Math. Nat.), CIII., 1 Abth., p. 153, 1894.

[2] H. de Vries. "Sur un spadice tubuleux du *Peperomia maculosa*" Arch. néerl. des sci. ex. et nat. XXIV., p. 258, 1891.

[3] The case usually quoted as a ring-fasciation in *Taraxacum officinale* appears to be of a more complex type than those here mentioned: according to Reichardt (Verh. d. k. k. Zool. Bot. Ges. in Wien., XIII, p. 1009, 1863) three rings of vascular bundles are present in the tubular scape.

As already mentioned, the structure here described belongs to the class of abnormalities known as ring-fasciations. In the ordinary linear fasciations such as are so frequently seen in *Asparagus officinale*, *Crepis biennis*, etc., the terminal meristem of the axis is broadened in one plane, remaining narrow in others: the resulting axis becomes ribbon-shaped in consequence. The peculiar radiate fasciation[1] is a simple variant of the linear, in which the lateral extension of the meristem takes place in more than one plane, so that the axis is strongly winged. In the ring-fasciation, however, the meristem is annular. At its inception it may be considered to arise by the sterilisation of the apical spot of the normal paraboloid meristematic region, leaving the peripheral cells still active. Further growth tends to widen the diameter of this ring of meristem and at the same time to increase the cavity within: the funnel-shaped axis is the result.[2]

Linear fasciation has often been pictured (as indeed the word fasciation implies) as the concrescence in a linear series of a number of individual branches which in the normal state would be free from one another. While there is no foundation in ontogeny for such a view, it is useful for the moment to regard ring-fasciation from a similar standpoint, for the sake of elucidating the vascular anatomy.

In the adjoining diagram (Fig. 4) six circles (drawn in thin continuous lines), are arranged to represent individual stems in contact with one another in a ring. In each stem is figured a number of normally oriented vascular bundles (xylem black, phloem left clear). If we now imagine all these contiguous stems fused together into a solid ring of tissue (heavily outlined in the diagram)

[1] H. de Vries. "The Mutation Theory" (Engl. Transl.) II., p. 497, 1911.

[2] L. Lutz explains in a similar way what appears to be an analogous case in the Phæophyceæ—the production of an infundibuliform branch in *Ascophyllum nodosum*. Bull. Soc. Bot. France LVI., p. 606, 1910.

we obtain, according to the concrescence theory, a ring-fasciation. Now assuming that the vascular bundles which lie near the points of contact of the component stems (those on the common radii in the figure) are obliterated, we are left with an external and an internal system of vascular bundles: those of the latter are fewer in number and have an inverse orientation. (In the diagram the the two systems are joined up respectively by dotted lines).

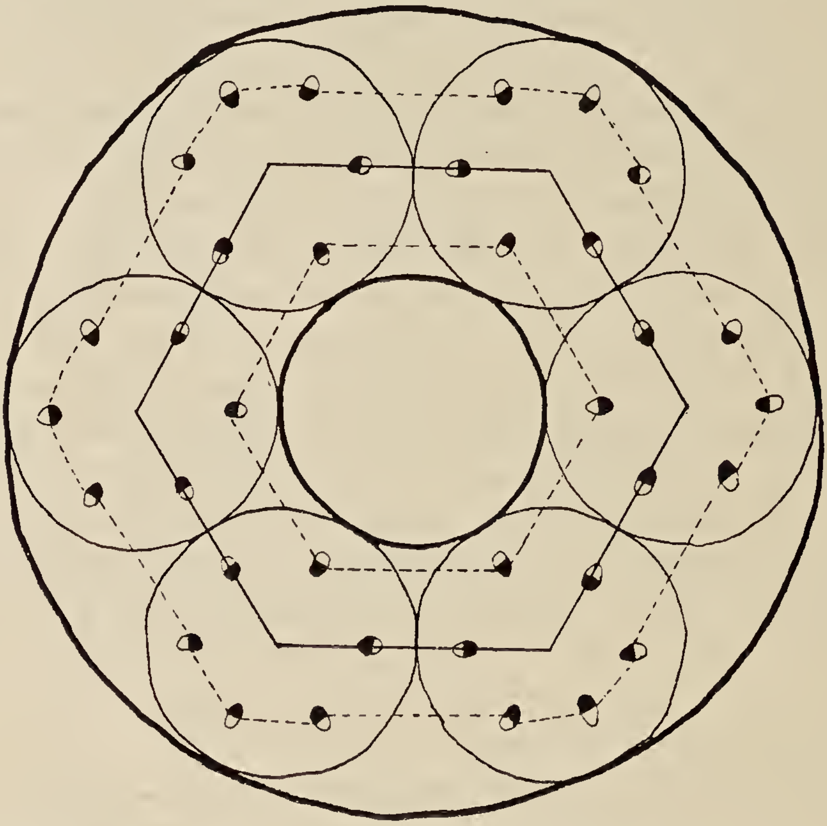

Fig. 4. Geometrical construction for ring-fasciation on the theory of concrescence.

Thus while denying that a ring-fasciation is actually produced by concrescence, we may obtain by this analytical method an insight into the origin of its anomalous structure.

It also appears that in certain cases a ring-fasciation may be produced by the invagination of the external tissues. This is the interpretation put by Richter[1] on certain abnormalities in *Helianthus annuus*. If we consider these two methods of the formation of ring-fasciations, we are forcibly reminded of the two rival theories that have been advanced to account for the medullation of the stele in Pteridophyta, Pteridospermæ, etc. The method of direct tubulisation described for the Mummy Pea may be compared with the theory of the intrastelar origin of the pith: while the method of invagination may be compared with the extrastelar interpretation. The parallel becomes more striking when it is recalled that in *Onoclea germanica* an epidermis and air may be included within the stem through invagination at a leaf-gap.[1]

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[1] P. Richter "Ueber Missbildungen der Blüthenkopfe der Sonnenblume." Ber. d. d. Bot. Ges. VIII., p. 231, 1890.

Moreover the peculiar arrangement of the tissues in ring-fasciations, with xylem lying between two zones of phloem, pericycle, endodermis and ground tissue, is singularly suggestive of the typical amphiphloic solenostele; and the gradual dwindling and final disappearance of the internal ring of bundles in the Mummy Pea when traced downwards may be compared with the similar dwindling of the central tissues in a solenostele until the protostelic condition is reached.

Although the value to be attached to such a comparison is necessarily slight, yet the general implication seems to be in favour of the view that medullation, like ring-fasciation may arise in different ways in different cases: (1) by the intra-stelar method, or direct tubulisation; (2) by the extra-stelar method, or invagination.

[1] E. C. Jeffrey "The Pteropsida." Bot. Gaz., L., p. 400, 1910.

CAMBRIDGE,
August, 1911.

PECULIAR SPORE-FORMS OF *BOTRYTIS*.

BY S. REGINALD PRICE, B.A.

(*Late Scholar of Clare College, Cambridge*).

[WITH EIGHT FIGURES.]

SOME material of *Botrytis*, exhibiting certain spore-forms of which no description has been found, has recently been under my examination.

Well developed sclerotia, black in colour and varying in length up to 12 or 14 mm. were found on the dead and dry stem of an Umbellifer, near Wellington, Somerset, early in April, 1911. From the character of the stem, and the flora of the spot examined later in the summer, there is little doubt that the host plant was the Hemlock, *Conium maculatum*. The sclerotia were freely giving rise to conidiophores and conidia, and were identified as belonging to *Botrytis cinerea* var. *sclerotiophila* Sacc. These sclerotia were formerly known by the name of *Sclerotium durum*. The general appearance of a piece of the stem with sclerotia, is shown in the photograph (Fig. 1), slightly reduced.

Some of the sclerotia when teased out and examined under the microscope, showed thick-walled spherical spore-like bodies, very much larger than the conidia, and borne quite near the surface of the stroma: other sclerotia were bearing conidia alone. Although I have not succeeded in inducing these spore-like bodies to germinate, their characters strongly suggest that they function as spores.

The wall of this peculiar spore-form is thick, as already stated, brownish yellow in colour, and slightly granulated on the exterior; while the contents are dense and granular with some oil globules. The spores are borne on septate hyphæ, which project from the body of the sclerotium (Figs. 2 and 3). In general these hyphæ resemble those which bear the conidiophores at their apices. Although the spherical spores are usually terminal, this is by no means invariably the case. Sometimes the hypha appears to grow again from the apical end of the spore, so that the latter assumes an intercalary position (Fig. 4). In other cases the free end of the hypha may form another spore, thus producing an intercalary and a terminal spore, separated by a short hyphal filament (Fig. 5). Others again show two spores in contact and the same arrangement as the last, but without the intervening hypha (Fig. 6).

The measurements are as follows:—

Diameter of spores - -	$35\text{-}71\mu$ (According to relative maturity, etc.)
Average diameter of fully developed spores -	$60\text{-}70\mu$
Average thickness of hypæ bearing the spores -	$16\text{-}18\mu$

Hanging drop cultures were made in pure water, and in "grape-extract," using the spore-forms as free as possible from conidia,

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Fig. 1. Portion of stem of *Conium*, with black sclerotia. About $\frac{2}{3}$ natural size.

Fig. 2. Portion of sclerotium showing resting spores and hyphæ. × 100 diam.

Figs. 3—8. × 350 diam.

Fig. 3. Single terminal spore showing nature of wall and contents.

Fig. 4. Spore in intercalary position.

Fig. 5. Two spores separated by single hyphal cell.

Fig. 6. Another common arrangement of two spores..

Fig. 7. Typical "organ of attachment" produced on germination of the conidia.

Fig. 8. The same. Younger stage.

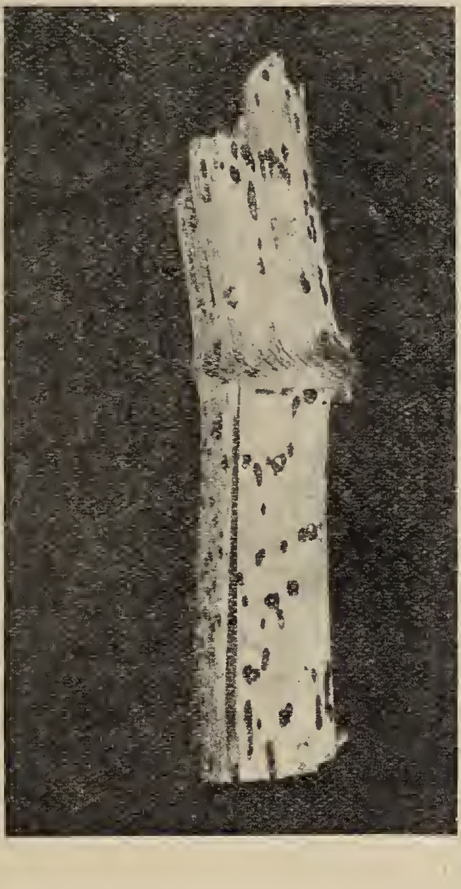
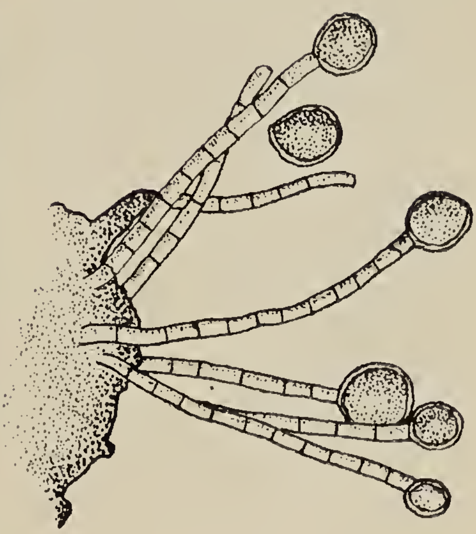


Fig. 1.



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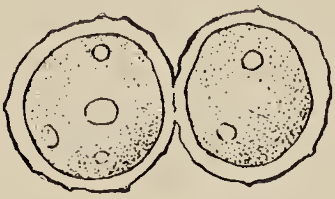

Fig. 6.

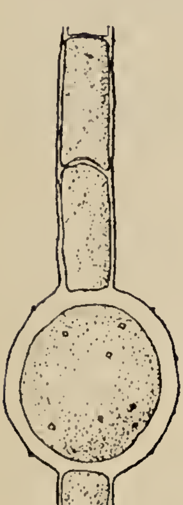

Fig. 5.

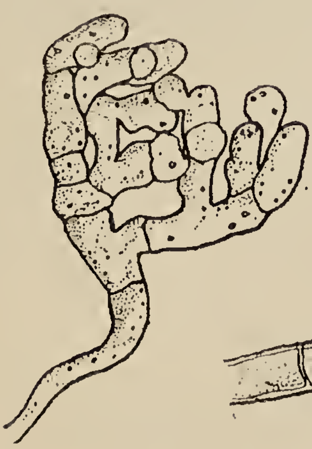

Fig. 7.

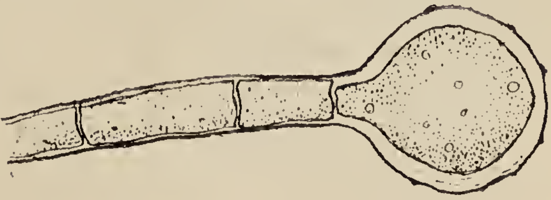

Fig. 3.

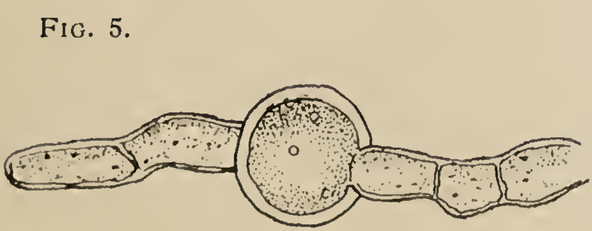

Fig. 4.

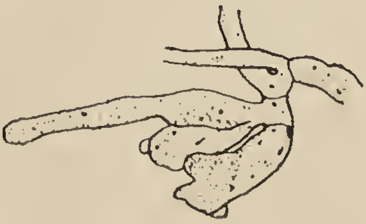

Fig. 8.

although it was impossible entirely to exclude the latter. The large spores, however, failed to exhibit any signs of germination. Any conidia that were present germinated readily and produced the characteristic "organs of attachment" in profusion, indicating that the fungus was in a normal condition (Figs. 7 and 8).

No account of exactly similar structures has been found, and since details of their germination and development are lacking, it is hardly possible to determine their real nature with any degree of finality.

Certain Oidial conditions of *Botrytis* described and figured by Istvánffi (2) seem to shew structures, perhaps somewhat of the same nature, but a detailed comparison indicates that there are important differences between them and the spore-forms now described. The spores under consideration are more definite in position and mode of occurrence than in Istvánffi's oidial fragmentation, and moreover they are borne on the sclerotia, whereas the oidia were produced from young artificial cultures in the filamentous state. There also appears to be a difference in the spore contents: Istvánffi describes the oidial contents as "du plasma extraordinairement transparent (et) écumeux," while the contents of the "resting spores" are "écumeux," but rather opaque and yellowish brown in tint. The spore diameter is about the same in each case (40-80μ for the oidia), and bearing in mind the different environment, the manner of formation is not altogether dissimilar.

The structures produced by the type of fragmentation described by Farneti (3) also appear to be different.

Istvánffi (2), Brooks (1) and others have shown how great is the plasticity of *Botrytis cinerea* under cultural conditions, and the present observations show that yet another spore-form may occasionally be present in natural conditions.

Whatever their homology, there seems little doubt that the structures function as resting spores of some type.

Certain stages in their formation, and similarities in position and branching between the hyphæ bearing resting-spores and conidia respectively, may indicate that the resting-spores are structures homologous with the upper parts of conidiophores, in which the sterigmata have become suppressed. This may have been influenced by external conditions, so that the incipient conidiophore ceased to function as such, but enlarged to form a food-storing spore, while later on, under more favourable conditions, the same sclerotium formed another crop of normal conidiophores. This manner of formation would explain the occurrence of the definite layer of resting-spores around the sclerotium, but the hypothesis is nothing more than a possibility deduced from the general morphology of the specimen.

There still remains the hypothesis that the spores are definite resting-spores, produced quite normally and in a definite manner at a certain stage of the life history under certain conditions.

Whatever the morphological value of these resting-spores, the case is more especially interesting since they occurred in a state of nature and not in artificial culture, so that they may be regarded as constituting a normal phase in the life history of the fungus.

I wish to express my thanks to Mr. F. T. Brooks, of Cambridge, for the assistance he has given me in this work, and to Mr. S. Mangham for the photograph for Fig. 1.

BOTANY SCHOOL, CAMBRIDGE.

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1. Brooks, F. T. Ann. Bot., 1908, pp. 479-487.
2. Istvánffi, Ann. de l'Inst. Cent Ampelogique Roy. Hongrois T. III, Liv. 4, 1905, p. 326, sqq.
3. Farneti, see Istvánffi (2), p. 326, and Atti del R. Instit. Botanico dell Univ. di Pavia, VII, 1901.

SKETCHES OF VEGETATION AT HOME AND ABROAD.

VII.—The Vegetation of the Island of Gothland.

By H. Hamshaw Thomas.

[With Plates IV and V.]

Introduction.

In the Baltic Sea, about 60 miles from the Swedish Coast, lies the Island of Gothland. Though in the Middle Ages it was one of the most important places in Northern Europe, it is now of no great commercial importance, yet it is of great interest to the botanist and to the antiquarian. As early as 1623 some of its more noticeable plants were described, while about a hundred years later Linnæus greatly extended the list of species. Since that time the flora has not lacked the attention of Swedish botanists and in 1897 Dr. K. Johansson[1] published an important paper dealing in an interesting manner with some of the ecological aspects of the flora. As far as I am aware, however, no survey of the vegetation of the island has been made on modern lines.

General Characters of the Island.

The Island is about 70 miles long and 20 miles across, the total area being about 1220 square miles; the population is about 52,000, and most of the inhabitants are occupied in agriculture. Visby, the ancient Hanseatic city, is the only large town, but the country is thickly studded with small villages, each of which usually possesses a beautiful little church. On the east of the island is a small port, Slite, and some of the Finland Line of steamers, sailing from Hull to Helsingfors, call there for passengers and cargo. Roughly speaking, about half of the island is covered by more or less primitive vegetation, chiefly pine-forests and marsh-land, but large tracts of original fen have been reclaimed and are now used as pasture for cattle: cattle-rearing is one of the chief industries of the country.

Physical Conditions.

Owing to its insular position the climate differs somewhat from that of the mainland of Sweden. The Ivy and Walnut, which are both rare in Sweden, grow here in many places. The average

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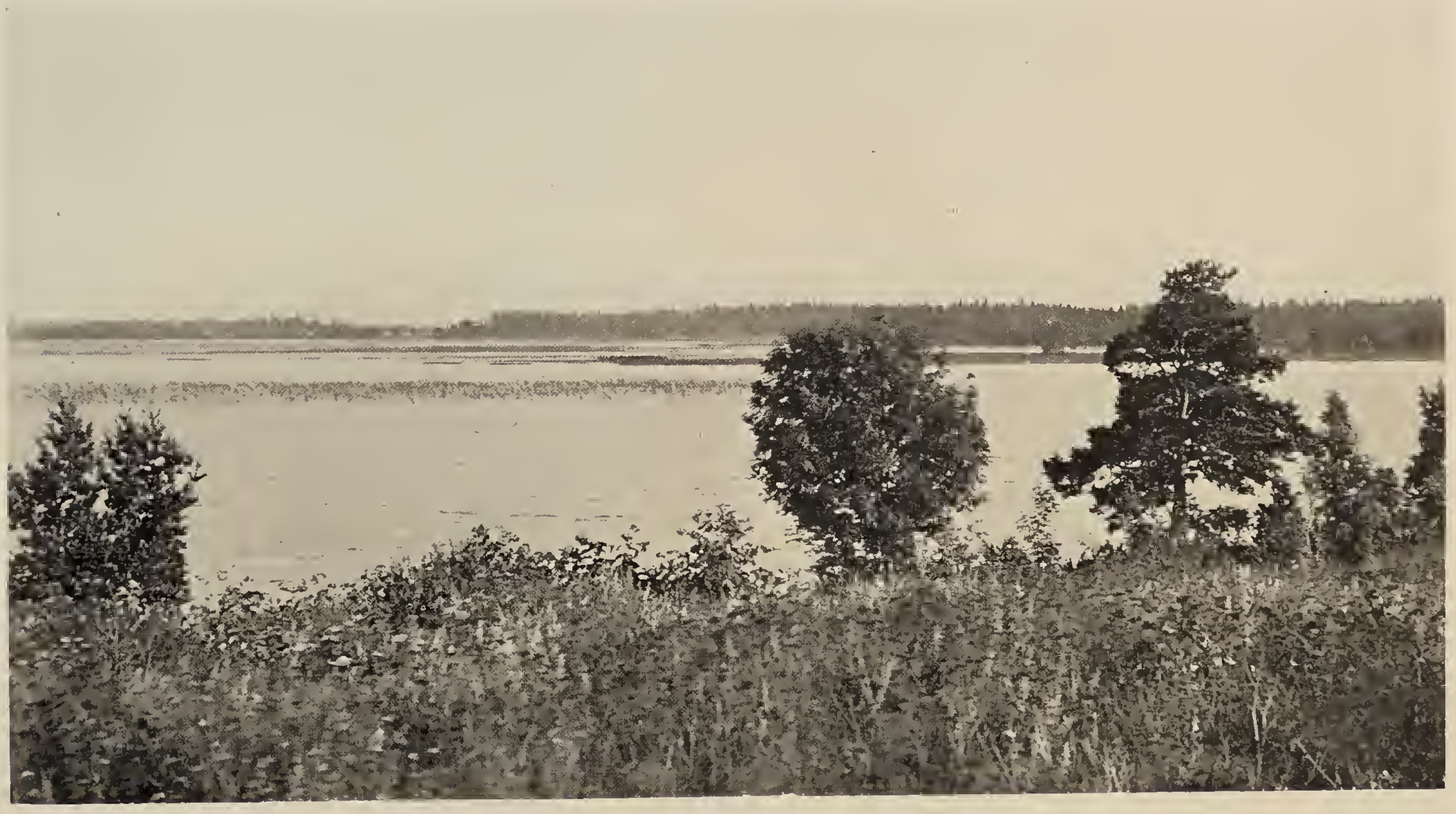
[1] Johansson, K. "Gotlands växttopografi och vaxtgeografi." K. Svenska Vet. Akad. Hand., Bd. 29, No. 1, 1897.



HAMSHAW THOMAS.--Vegetation of Gothland.

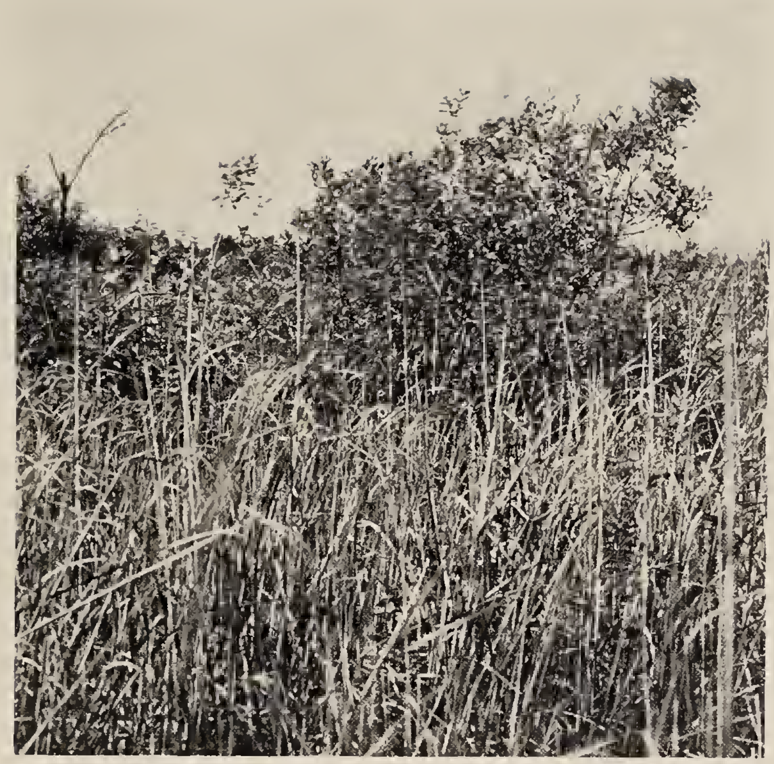


Fig. 1.

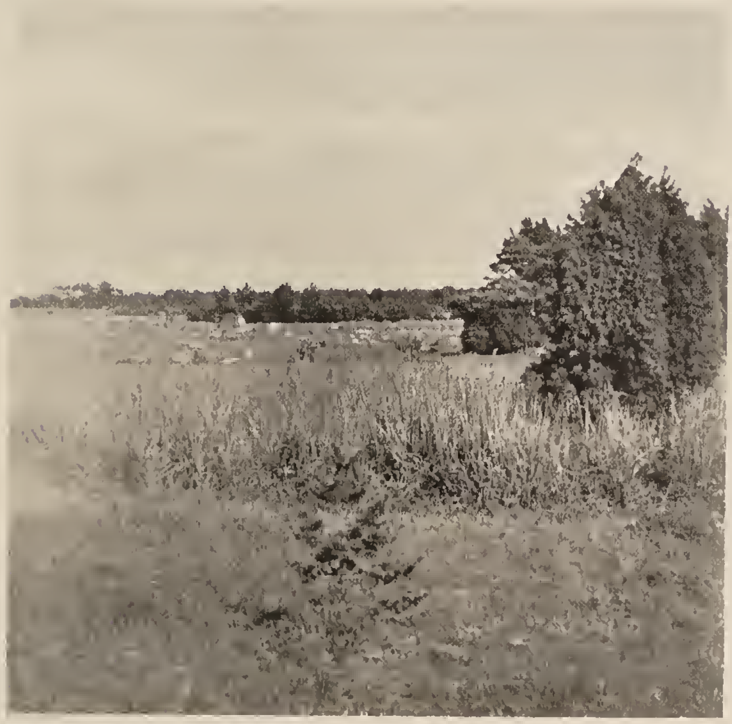


Fig. 2.

Hamshaw Thomas.—Vegetation of Gothland.

temperature (6·4°C) does not seem to differ very much from that of the mainland at Lund, but probably the winters are milder; the rainfall (472 *mm.*) is somewhat less than at Lund. In spite of the somewhat similar climatic conditions, the Gothland flora presents some striking differences from that of the mainland. This is probably due to the geological structure of the island.

The underlying rock of which the island is composed, is almost entirely Silurian limestone which is very well developed and forms nearly horizontal beds. There are steep cliffs on the western coast-line but the whole of the interior is very flat and forms a plateau about 40 metres above sea level. The underlying rock is generally covered with a considerable thickness of glacial drift of varying composition, but chiefly of a sandy and gravelly nature, though the soil is usually calcareous. In many places the drift is now absent and the limestone appears at the surface and bears a "limestone pavement" flora. Much of the cultivated land in the island has been derived from what must have formerly been extensive marshes or lakes. These have been drained and the original lakes have either disappeared or have been reduced to the size of ponds. The land covered by the sandy drift was in most places occupied by pine forest and some of this country also has been reclaimed by man.

FLORISTICS.

Dr. Johansson has given a careful analysis of the flora in his paper. He has distinguished about 1008 species of flowering plants and ferns, but of this number about 100 are species of the genus *Hieracium*. A few of the plants do not occur elsewhere in Sweden, though the flora in general is very closely related to the flora of the island of Öland, nearer the Swedish coast, and also to the flora of the Russian provinces on the other side of the Baltic, where similar Silurian rocks occur. Many of the plants, however especially those of the pine forests, occur also in localities on the mainland extending northwards for a considerable distance.

GENERAL ECOLOGICAL DIVISIONS.

Johansson has distinguished the following plant communities (växtsamhällen):—

1. Sea plants.
2. (*a*) Fresh-water plants.
   (*b*) Water-loving swamp plants.
3. (*a*) Marsh plants (proper).
   (*b*) Limestone bog plants.

4. Sea Shore plants.
5. (*a*) Field plants.
   (*b*) Ruderals.
   (*c*) Hedgerow (Kulturgränsens) plants.
6. Pine forest.
7. Other mesophytes of meadows, deciduous woods, etc.
8. Rock plants.
9. Sand plants.

According to the modern nomenclature of English ecologists, the natural vegetation of the island may perhaps be considered as belonging to four or five formations, *viz.*, fen and calcareous bog formations, sandy drift forest formation, limestone rock and pasture formation, salt marsh formation. During a short visit to the island in July of this year I had the opportunity of noticing some of the chief characteristics of the first four of these. It may be of some interest if I give a short account of them.

THE FENLANDS.

A considerable portion of the lower-lying part of the country is dotted with small patches of fenland, and if, as may reasonably be supposed, the intermediate flat cultivated land was formerly fen also, almost half of the country would have originally been included in this formation. The existing marshland lies either round small lakes or along the course of the streams. Its origin may be accounted for in several ways. It was probably derived from a series of lakes in a badly drained partially submerged country. This may have originated at a period when the surface of the land was not so high above the sea and the rivers were consequently near their base level, and when the precipitation was greater. The level of the land is known to have been lower during early post-glacial times than to-day, since raised beaches of the "Littorina sea" are found, which were formed in comparatively recent Quaternary times.[1] The lakes might also be due to the partial solution of the underlying limestone, or to the occurrence of bands of marl in the underlying rock. Again, many lakes are partially surrounded by sandy drift, and swamp may have been due to the formation of an impervious layer in the sand by the precipitation of iron compounds (moor pan). It is quite probable that more than one, or even that all of these causes have operated to give rise to lakes and fens.

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[1] The historical development of the flora of Gothland has been studied by Sernander. *Studier öfver den Gotländska vegetationens utvecklingshistoria. Akad. Afh. Uppsala, 1894.* In the "Littorina age" of post-glacial time, there was an extension of the sea in many parts of West Europe. The Baltic had probably been hitherto a fresh water lake (the "Ancillus Sea") but now became much more extensive. The lower layers of peat in Gothland date from these Ancillus and Littorina periods (named after the characteristic molluscs); they contain a large number of plants, *Phragmites* being abundant. It is likely that the Littorina subsidence came about the end of the neolithic period.

The largest lake existing at the present time is Tingstäde träsk (see Pl. IV) which is about 3 *km.* long and 2 *km.* across. Near the side where there is least vegetation its bottom seems to be formed of a very calcareous mud. The water is quite alkaline and appears to be shallow in all parts. A considerable portion is colonised by *Phragmites*, while islands of *Cladium Mariscus* are also seen. The *Phragmites* forms thick beds on the eastern side and we doubtless have here the first stage in fen formation. This lake adjoins a considerable tract of reclaimed fen on one side, known locally as "myr," while a few miles away in the neighbourhood of Martebo a very extensive marsh formerly existed which was probably part of the same series of fens. The Martebo marsh has now been drained and most of it is under cultivation, though here and there we find the remains of many small lakes, some of which are surrounded with interesting vegetation.

I was able to examine the remains of one of the best of these small lakes, Binge träsk. In July the site of the lake was marked by an extensive tract of dry powdery peat. In places there were patches of *Phragmites*, which seemed to be still growing vigorously, some plants of *Cladium*, almost dead, and a number of bushes of *Salix repens*. The relative vigour of the *Phragmites* was doubtless due to its deeper root-system. To one side of this tract was a thicket with dense vegetation apparently little affected by the drainage and probably still retaining most of its original features. Much of it was birch and willow scrub, but among it were patches of very wet spongy bog with the water table less than six inches below the surface of the ground. Since the dry bare peat almost certainly represents the last vestiges of the former lake and was in fact probably recently covered with water, it seemed curious that it should be quite dry and powdery, at the same time that the ground a few dozen yards away, which had been long above the surface of the lake and was thickly covered with vegetation, was absolutely saturated with water.

The most probable explanation of this fact rests on the relative depths of the peat. Where the peat is shallow the water gets through and quickly percolates away into the underlying limestone rock, but where the peat is very deep this process would be very slow. Owing to the impermeability of peat there would be little lateral movement of water, and thus the water table might well be at a much higher level where the peat was deep than at a point a few yards away where the peat was shallow. This explanation would be supported by the character of the flora, for while the deep peat on one side of the lake bears fen-carr[1] vegetation the shallow peat on the other side of the lake is characterised by a flora of the limestone bog type.

The vegetation of the spongy bog presented an aspect almost identical with that of many of the East Anglian fens. The surface was covered in the wetter parts by a raft-like mat of *Cladium* rhizomes, with mosses, *Carices* and some *Phragmites*. The following plants also were abundant:—

Peucedanum palustre.	*Pedicularis palustris.*
Comarum palustre.	*Orchis incarnata.*
Menyanthes trifoliata.	*Lathyrus palustris.*

In many places the last remnants of pools occurred, some of which contained small leaves of a *Nymphæa*, while others were patches of mud with *Eriophorum vaginatum*, *Equisetum palustre* and *Drosera longifolia*. As one walked over this the whole surface quaked and often sank below water. The underlying water was tested with red-litmus paper, and gave a blue coloration, but only after several minutes. Where the surface was a little more solid, bushes of *Myrica Gale* are plentiful, with *Lysimachia*, *Galium uliginosum*, *Cirsium palustre*, etc. *Spiræa Ulmaria* occurs plentifully, but is confined to the drier spots. These remnants of bog were more or less surrounded by carr consisting of a dense mass of shrubs about 8-12 feet high (cf. Pl. V, fig. 2). The shrubs were chiefly birch (*Betula verrucosa*), willow (*Salix cinerea* and *pentandra*) and some *Rhamnus Frangula*. The birch is less abundant in the wetter places, but *Alnus* is comparatively rare. It may be noted that the marsh fern *Lastræa Thelypteris*, among many other marsh plants, occurs in some of these carrs. It would seem as if we had here a series of stages in the succession of vegetation from the open water of the lake to the birch thicket. Both the dominant plants, the associated species and the apparent succession are very similar to those seen in our East Anglian fens. The occurrence of these plants is doubtless largely determined by the physical conditions of the habitat, especially the calcareous and alkaline character of the water. Very large tracts of country bearing similar vegetation formerly existed and still bear the name of "myr," but the fens are now rapidly disappearing. In some places the drainage dykes show peat to a depth of 4 feet or more, resting on a bed of marl, but detailed observations on this point are wanting. The *Cladium* fens have, by drainage, been turned into rank pasture for cattle and the widespread use of this plant for thatching cottages has practically died out.

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[1] See M. Pallis in *Types of British Vegetation*, Chap. X, p. 236.

CALCAREOUS BOG.

While the fen vegetation, as just described, is so like that of our English fens, it passes over into a type of calcareous bog which is quite unknown in East Anglia, though similar to a type occurring in the North of England. One of the most characteristic plants of this association is *Primula farinosa*, which often forms a pure open association. The closed vegetation of this type contains abundant *Schœnus nigricans* (or *ferrugineus*) and *Eriophorum latifolium*, while the following plants are very common:—

Tofieldia calyculata. *Orchis incarnata.*
Epipactis palustris. *Juncus obtusiflorus.*
Seslcria cærulea. *Drosera longifolia.*
Pinguicula vulgaris.

No critical observations on the nature of the soil could be made, but from casual inspection it appeared to be much more calcareous and less peaty than that of the fen. Two cases were noticed where one shore of a lake had vegetation of the *Phragmites-Cladium* fen type, while the opposite shore had vegetation of the limestone bog type. One of these was Tingstäde träsk. The northern shore is bounded by a flat of soft grey mud which was being colonised by *Schœnus ferrugineus.* Further away from the water *Drosera* and *Eriophorum* were very abundant, the vegetation being still of the open type. This passed gradually into closed turf-like vegetation, which would scarcely ever be submerged except in the wettest seasons. In this turf the species mentioned above were very frequent, while several small bushes of *Juniperus*, *Rhamnus Frangula* and *Salix* sp. occurred. In places where lakes had been drained the pine forest seemed to be quickly advancing over their margins. Seedlings of Pines and Juniper were springing up in great numbers in some of these localities (Pl. V, fig. 2).

It might be suggested that we have here two parallel developments of succession: (*a*) Reed swamp passing into fen and ultimately becoming birch thicket where the peat is thick and moist; (*b*) Calcareous bog passing into Pine forest where the soil is dryer and more calcareous and the peat thin. In view of this it might be more correct to place the limestone bog in a separate formation, but it is nevertheless very closely allied to the fen vegetation proper. In another locality which I saw there was an interesting patch of limestone bog forming a tussocky turf of grasses with much *Schœnus* and *Eriophorum* and an interesting series of orchids, viz.:—

Habenaria odoratissima. *Orchisi ncarnata* var. *Traunsteineri.*
Epipactis palustris. *Orchis pyramidalis*, etc.
Herminium monorchis.

Some *Utricularia* was growing in a pool in water which quickly turned red-litmus paper blue. Many pines were also springing up here, seedlings from the pine woods which surrounded the place.

This limestone bog vegetation bears considerable resemblance to some of the calcareous bogs of Teesdale. Professor Lindman of Stockholm informs me that much of the bog vegetation of Gothland closely resembles the vegetation round Haweswater in Lonsdale (North Lancashire), a locality which I have not yet seen. The examination of such an area as has been described tends to show that the physical and chemical factors of the soil which limit existence of the floras of our northern limestone bogs and of the East Anglian fens, are more nearly related than might be supposed.

The Pine Forest.

Gothland, like the mainland of Sweden, is a typical forest region. Trees, usually pine and birch, spring up wherever there is any available space, and extensive forests occur. On the mainland, where the rock is mostly granitic and very compact, trees are able to colonise rocky spots which are almost bare of soil save for a few small pockets of humus, but in Gothland, where the limestone rock is well jointed and very porous they are unable to do so. Good forests are, however, found on the sandy and gravelly tracts of drift and in some places on the dry peaty deposits. Johansson divides the forests into two types, one characterised by an abundance of spruce fir, the other by the Scots pine; some smaller deciduous woods occur in the south, chiefly of birch and rowan (*Sorbus Aucuparia*). The spruce-woods occur on the more loamy soils and contain such ground vegetation as *Melampyrum sylvaticum*, *Oxalis Acetosella* and *Viola sylvestris*.

Among some of the pine-woods numerous remains of small peaty lakes occur; where the water had disappeared and the former lake-bottom was covered with grass, seedlings of pine and juniper were common (cf. Pl. V, fig. 2) and the forest seemed to be spreading over the whole tract. It would seem likely then that much of the present pine forest belongs to the fen succession. The occurrence of pine on these tracts, and also as a colonist of the calcareous bogs, indicates clearly that it is by no means a calcifuge. But the typical pine forest occurs on the sandy soil, tracts of which are found everywhere, and here it probably forms the ultimate stage of the psammophilous plant succession. The trees are chiefly *Pinus sylvestris* with but little spruce and birch. Shrubs are represented by *Juniperus communis* and *Taxus*. The ground flora contains *Pteris aquilina*, *Calluna vulgaris*, *Epilobium angustifolium*, etc. in the shadier woods. A number of species of *Pyrola* occur, and on the roadside banks through the woods I noticed much *Vaccinium Vitis-idæa*, *Cotoneaster integerrima* and low creeping masses of *Arctostaphylos*. The ground is often covered with creeping Ivy. The woods grow right on to the sea-cliffs in some places, but near the sea the trees show a stunted appearance and isolated trees often have a marked one-sided growth. In one of the dry woods on a very stony soil on the cliffs, there were a great many plants of *Epipactis rubiginosa* and also much *Anemone hepatica*.

In the more open places on the dry sandy soil we see many typical xerophytic plants with enormously well developed root systems. Exposures of bare sand support only a few plants such as *Scleranthus perennis*, *Rumex Acetosella*, *Sedum album*, etc. Where the vegetation was less open *Gnaphalium sylvaticum* occurred in large quantities, with *Erythræa*, *Centaurium Fragaria vesca* and numerous grasses (e.g., *Agrostis canina*). In the spring ephemerals such as *Veronica verna* grow here.

ROCK PLANTS.

In many places the surface of the underlying rock projects through the covering of sandy drift and forms a very unfavourable substratum for plants. These spots, however, support vegetation of an interesting type. The first plants to obtain a footing in the cracks of the bare rock are mosses, quickly followed by *Sedum album*. The latter is very abundant on the barest places: its prostrate stems creep over the surface bearing the reddish fleshy leaves and conspicuous inflorescences and sending down adventitious roots which find their way into the joints and cracks where a small amount of humus may have collected. When a little humus has collected on the rock, *Galium verum* and *Thymus Serpyllum* are abundant, the latter showing its creeping tufted habit. A variety of other plants occur, e.g., *Saxifraga tridactylites*, *Cerastium* spp., many species of *Hieracium*, *Aquilega vulgaris* with flowers of various shades of purple and blue. *Geranium robertianum* and *Pastinaca sativa* occur plentifully in the open vegetation of rock places.

OTHER ASSOCIATIONS.

Near Visby much of the surface above the cliffs has been at one time quarried for stone; in many places considerable areas are covered with rubbly material with some patches of bare rock and some patches of shallow turf. The quarrying operations probably ceased more than four centuries ago so that the vegetation here may be considered as fairly natural. From somewhat casual inspection it would appear that these tracts were colonised, first by mosses and *Sedum*, followed by *Thymus* and *Galium*: then many isolated plants of *Hieracium*, *Aquilegia*, *Geranium*, etc., appear, together with large quantities of *Cynanchum vincetoxicum*, an interesting Asclepiadaceous plant. This plant has woody stems about a foothigh and dark green leaves. With it, and where there is more soil between the stones, we get a considerable growth of low shrubby bushes, many of them procumbent. The following are common:—

Prunus spinosa.
Cratægus monogyna ?
Juniperus communis.
Cotoneaster integerrima.
Berberis vulgaris.
Arctostaphylos Uva-ursi.
Rosa, spp.
Sorbus fennica.

Where the ground has been undisturbed and a thin layer of soil covers the rock there is a vegetation of the limestone pasture type, containing various Grasses and Hieracia with

Anthyllis vulneraria.
Asperula tinctoria.
Pulsatilla patens.
Poterium Sanguisorba.
Helianthemum Fumaria.
Geranium spp.
Ononis repens.
Cnicus acaulis.
Cerastium glutinosum.
Allium Schoenopersum.[1]

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[1] This species was in fruit and in most cases the seeds appeared to be sprouting while still attached to the capsule. Some of the seedlings were 2 to 3 cms. long in spite of the dryness of the weather.

Another plant very characteristic of the limestone pasture in England often occurred, viz., *Spiræa Filipendula*, but only in the damper places where the soil was thicker. Scrubby bushes of *Cotoneaster*, *Juniperus*, etc. were common on this chalky pasture, and dwarf pines, also occurred in some numbers. These had a rather uniform height of about 4 feet and gave the impression in some places that they might have been planted, but it is scarcely probable that this was the case and their dwarf size must be partially attributed to the dry shallow soil.

In addition to the plant-associations already mentioned the island possesses a number of maritime plants, but these occur chiefly on the east coast and I did not see them. I must, however, just mention some of the commonest weeds of hedgerows and waste places. These are very conspicuous because of their beautiful colours, and the most noticeable among them are *Cichorium Intybus* and *Echium vulgare*. They occur in great abundance in the waste places round the city walls at Visby and by the roadsides. The *Echium* has inflorescences often 18 inches or more in height and gives rise to masses of blue colour. Other Boraginaceous plants, e.g., *Anchusa* and *Cynoglossum* are also common. One of the most noticeable weeds of cultivated land is *Anthemis tinctoria* which when undisturbed grows in large clumps and bears numbers of brilliant golden flowers. The blue *Centaurea minor* is one of the commonest cornfield weeds, and the wild roses of Gothland are famous and contribute largely to the beauty of the flora.

It is hoped that the above will give some idea of the vegetation of the Island as it appeared from very brief visits to some few of the typical localities. Though there are so many striking points of similarity between the vegetation of Gothland and that of England, there are doubtless many differences, which may be even greater than I was led to suppose, because in any hasty comparison the resemblances are more obvious than the differences. The absence of most deciduous trees is, of course, a very great difference. A more careful and detailed comparison by an expert ecologist would be very interesting, and it is to be hoped that this will be made before the last traces of the Gothland fens disappear. I believe that such a comparison would go far to confirm the view that the chemical and physical nature of soil is a factor of the greatest importance in determining the geographical distribution of plants, and that in relatively small areas the soil has a much greater influence than the physical configuration of the land.

EXPLANATION OF PLATES IV AND V

Illustrating Mr. H. Hamshaw Thomas' Paper on "The Vegetation of the Island of Gothland."

Plate IV. View of Tingstäde träsk, showing open water being colonised by Phragmites—the dark patches in the distance are *Cladium*. The Pine forests fringing the further side of the lake are seen, and in the foreground some seattered trees of *Pinus* and *Sorbus aucuparia*, with a ground flora of weeds such as *Anthemis tinctora*, *Echium vulgare*, etc.

Plate V. Fig. 1. View in Binge träsk, showing part of the spongy bog dominated by *Cladium*, behind are bushes of *Salix cinerea*, forming the outlying portion of the large carr.

Plate V. Fig. 2. View near Martebo, showing a dried-up lake fringed with pine forest. In the foreground some remains of *Cladium* are seen and also one or more seedling pines. Pines and Junipers were springing up in large numbers there.

THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

I. The Inception of the Excursion.

THE study of Phytogeography, from the very nature of the material with which it deals, demands a comparison of the flora and vegetation of different parts of the earth's surface, and this is equally true of the floristic side, which is concerned with the distribution of species, and of the ecological side, which deals with the distribution of vegetatation, *i.e.*, of plant-communities. Floristic botanists, owing to limitations of time and money, largely depend for their material upon herbaria-collections of dried plants from different parts of the world. In times past at any rate, many of the most eminent are said to have been almost unable to recognise living plants of species with which they were perfectly familiar in the herbarium, and it is notorious that by far the larger number of diagnoses of species are founded upon dried material alone. The divorce of the study of systematic botany from the study of plants as living organisms thus resulting, has very often been recognised and deplored. There is no need to labour the point again. The formation and study of herbaria are of course essential, and even apart from limitations of time and space, could never be wholly replaced by personal investigation in the field and laboratory. But it will be very generally admitted that the systematic botanist who spends little time in the field and never becomes thoroughly acquainted with living plants at first hand must necessarily be ill-equipped for his task. Of course very many systematists actively pursue, and always have actively pursued, their studies in the field, both in their own and in other countries. Important light is always thrown on the flora of a country by the study of the floras of the neighbouring countries, and indeed such study is essential to its proper understanding. Hitherto no mechanism has existed for the investigation of a flora by botanists from neighbouring countries in company with native botanists. Isolated visits to this end have no doubt been frequent, but carefully organised international excursions have hardly existed, except indeed incidentally in connexion with international congresses. In recent years the most important of these have been organised in connexion with the International Congress of

Botanists at Vienna in 1905, the International Congress of Geography at Geneva in 1908, and the International Congress of Botanists at Brussels in 1910.

The Swiss botanists are particularly energetic and successful in organising botanical excursions in connexion with their botanical curricula; they regard such excursions as an essential part of the training of their own students; and they always welcome the presence of foreigners in the kindest way, and do everything that enthusiasm and the utmost goodwill can suggest to facilitate the study of their beautiful native vegetation. Nor have they confined their efforts entirely to the needs of their own students or to their own country. The excursion through Switzerland in connexion with the International Congress of Geography at Geneva in 1908, organised and conducted by Professor Schröter of Zürich, was in all respects a model of what an international excursion should be, and suggested to the present writer the idea of a similar excursion in the British Isles, which has been carried out this year, and is the occasion of the present article. The Swiss excursion of 1908 was attended by Professor Flahault of Montpellier, by Dr. and Frau von Hayek of Vienna, by Dr. Ostenfeld of Copenhagen, by Professor Rothert of Odessa, by Dr. Scharfetter of Villach and by the present writer, as well as by several Swiss botanists under the leadership of Professor Schröter and Dr. E. Rübel of Zürich. It lasted eleven days, during which Mount Pilatus, the Sihltal at Einsiedeln, the lakes of the Canton Ticino and the neighbouring part of Italy, the Bernina region, and the neighbourhood of St. Moritz in the Engadine were visited. In writing of the work of the Swiss in this connexion mention should be made of the "Naturwissenschaftliche Studienreise" organised by Professor Rikli of Zürich in the spring of every alternate year. Visits have been made to the Balearic Islands, to Madeira and the Iberian peninsula, and in the spring of 1910, to Algeria. Next summer there is to be an expedition to the South Russian steppes and to the Caucasus. These expeditions, intended primarily for the students of the Federal Polytechnic at Zürich, are nevertheless open to foreigners and others who have some definite scientific object to pursue, and are most useful in affording opportunities of visiting various places in Southern Europe and neighbouring regions at a minimum of cost, and in company with fellow-workers. The object of these excursions is not however primarily botanical, but includes geology, zoology, ethnology and so on, though the interests of plant-geographers play a considerable part in the choice of route and in the general arrangements. Professor Chodat of Geneva, also conducts distant excursions for his students once or twice a year.

The rise and spread of the study of vegetation which has been so marked a feature of recent years, demands, even more urgently than floristic botany, the organisation of expeditions of this kind. While the student of the distribution of species can depend more or less on herbaria and on floras, which at least give him systematised, though often inadequate, information as to the species of plants which occur in other countries, the student of the distribution, structure, relationships and development of plant-communities has to depend upon published descriptions and photographs of vegetation, which, even at the best, do not convey to him an idea of the phenomena involved in any way comparable with that which he can obtain on the spot, especially with the assistance of botanists who have actually studied the vegetation in question. In the present somewhat rudimentary state of evolution of the concepts and corresponding language of ecological plant-geography, this difficulty of obtaining clear and definite ideas of the vegetation of other countries without visiting them is necessarily very great. Workers in different countries use different names for the same thing and the same name for different things; they are frequently not at one as to the fundamental *differentia* of the units they employ. When we add to the difficulties arising on this score the fact that while vegetation all over the earth has, beyond question, fundamental similarities in regard to its structure, differentiation and relation to habitat, yet these similarities are greatly obscured by certain peculiarities of climate, soil, and floristic distribution, and even more by the results of the long-continued activity of man in the countries which have an old civilisation, it is not surprising that, with the best will in the world, keen students of vegetation in different countries should often altogether misunderstand one another's writings.

To overcome such difficulties much patience and determination and frequent interchange of visits are absolutely essential. It was with the object of making a definite beginning in this direction that the British Vegetation Committee, at the suggestion of the present writer, decided, in December, 1908, to attempt to organise an international excursion in the British Islands, "than which" to quote the words of the preliminary circular issued in January, 1910, "it is believed there is no easily accessible European country less known to Continental plant-geographers." After a good deal of preliminary correspondence and discussion as to the most suitable date, it was decided, in December, 1909, to fix on the month of August, 1911, and a rough outline of the places to be visited was drawn up and embodied in the circular referred to. The purpose of the excursion was defined as that " of visiting under the guidance of botanists who have specially studied them, the principal types of vegetation to be met with in the British Isles." Thus, in accordance with the objects which the British Vegetation Committee exists to promote, the aim of the excursion was defined as ecological rather than floristic. It was also decided that the the size of the party must be strictly limited, so that no public announcement was made, but the preliminary circular took the form of an invitation addressed to a selected list of foreign plant-geographers of distinction. The response was unexpectedly unanimous. With one exception all the botanists addressed provisionally accepted the invitation, and it thus became clear that the excursion would certainly not fail from lack of support. Later on, however, after the issue of a fuller programme in March, 1911, several of those who had provisionally accepted found that they would be prevented from coming by circumstances which had arisen since their original acceptance, and accordingly invitations were sent to others. At the last moment Professor Warming was kept at home by serious illness, from which all ecologists will be glad to learn that he has now happily completely recovered, Dr. Weber by unexpected circumstances and Professor Flahault by domestic considerations. It was with the greatest regret that the Committee learned that these three distinguished men could not after all be present, for to none more than to Professors Warming and Flahault does the recent growth of British ecology owe its stimulus and inspiration, while the absence of Dr. Weber from an expedition through a country possessing such extensive peat deposits as the British Isles, was certainly a very serious loss. The party eventually consisted of eleven foreign guests, about the number which was originally contemplated: Professor and Mrs. Clements of Minneapolis, Professor and Mrs. Cowles of Chicago, Professor Drude of Dresden, Professor Graebner of Berlin, Professor Lindman of Stockholm, Professor Massart of Brussels, Dr. Ostenfeld of Copenhagen, and Dr. Rübel and Professor Schröter of Zürich. Besides these Mr. G. Claridge Druce of Oxford, representing British floristic botany, was present during the whole tour, and various members of the

Committee accompanied the party during different portions of it, the local guides being in nearly every case those members who had carried out special studies on the vegetation visited. The present writer, who acted as general director of the tour, accompanied the party throughout. The number of the party varied between fourteen and twenty-two. The tour lasted four weeks, and a fifth week was spent at Portsmouth during the meeting of the British Association.

The scheme of the Committee included an attempt to supply the foreign visitors with information designed to enable them to obtain the greatest possible result from the tour. In the first place a book was prepared, under the editorship of the present writer, giving a systematic account of the vegetation of the British Isles.[1] The sections dealing with the different types of vegetation were in nearly every case illustrated by descriptions of the areas to be visited on the excursion, written by members of the Committee who had studied these areas. A copy of the book was presented to each foreign member of the party. A pamphlet of 32 pages was also prepared, containing "Descriptive Notes on the Topographical and Geological Features and on the Vegetation of the Route" written by the different local guides and containing full references to *Types of British Vegetation* and other relevant literature. Owing to great pressure of work involved in preparing the book and organising the excursion the editing of these "Descriptive Notes" left something to be desired, and the notes were not all they might have been in the way of uniformity and completeness. Finally a "Business Programme," containing general information, a skeleton programme of the tour, with names of Hotels, times of trains, etc., a map of the route and a list of members of the party, was prepared, and this was certainly of great use. The departures from the programme indicated were very slight.

Some permanent published record of the tour seems required, and an outline account of the doings of the party is subjoined. In the next number of this journal an account of the "Floristic Results of the Excursion" by Mr. G. Claridge Druce will appear, and in subsequent numbers it is hoped to publish some impressions by various foreign members of the party.

[1] Recently published by the Cambridge University Press under the title of *Types of British Vegetation*. Price 6/- net.

II. DETAILS OF THE EXCURSION.

The party assembled in Cambridge on Tuesday, August 1st. The morning was spent at the Botany School, and lunch was taken in the hall of Emmanuel College by permission of the Master and Fellows. The afternoon was spent at the Botanic Garden, round which the party were conducted by the Curator. Afterwards Dr. Moss demonstrated the numerous species and varieties of *Ulmus*, on which he had recently been working, to be met with in the Backs.

On the morning of Wednesday, August 2nd the party met on Sheep's Green and spent some time examining the riverside and submerged vegetation of the Cam, where the submerged forms of many of the common riverside plants were specially noted. The river was then ascended in punts and canoes as far as Grantchester, where the party were entertained at lunch by Mr. and Mrs. Tansley. In the afternoon some of the Colleges were visited and in the evening a dinner was given by Professor Seward and Mr. Blackman in the Combination Room of St. John's College.

A very early start was made on August 3rd, the party leaving Cambridge by the 6.45 train for Norwich and Brundall, where it was joined by Miss M. Pallis, who is engaged in a very thorough study of East Norfolk vegetation, and who acted as local guide. The much shrunken remnants of Surlingham Broad, situated in a bend of the River Yare, were first visited by boat. The old Ordnance Map published in 1838 shows this broad as a wide sheet of water. The aquatic vegetation, the reedswamp and fen are all characteristic of the Yare valley type. The broad is strongly affected by the rise and fall of the tide so that the "hover" or floating reedswamp dominated by *Glyceria aquatica* sometimes rests on the muddy bottom and sometimes floats over three or four feet of water. The fen and incipient "carr" (fen wood) with its considerable variety of shrubs were cursorily inspected. The party then returned to Brundall, proceeded by train to Buckenham, and after lunch at the Buckenham Ferry Hotel visited Rockland Broad, also by boat. Rockland Broad is the last broad in the valley of the Yare. Here very fine swamp carr (woodland which has established itself on reedswamp) was visited, and the absolutely natural condition of this type of vegetation greatly pleased the members of the party. Professor Massart obtained some excellent photographs. There was some discussion as to the rôle of *Phragmites vulgaris* in relation to fen and reedswamp. After returning to Buckenham the party took train to Yarmouth, passing across considerable tracts of pasture developed on loam and probably occupying the site of saltmarsh which originally developed in the old estuary of the Yare. Supper was taken in Yarmouth and the party then proceeded by train to Hemsby and Sutton, where the night was spent.

On Friday morning Sutton and Barton Broads (belonging to the River Ant) were visited in boats. The distinctive feature of this system of broads is the widespread association of *Scirpus lacustris* and rooted "floating-leaf" aquatics. Professor Cowles remarked on the great similarity of this vegetation to certain North American aquatic vegetation, the plant-forms, the genera and even many of the species being identical. The aquatic association of

Stratiotes Aloides is also remarkable, occupying a large extent of Barton Broad. These aquatic associations are rapidly filling up the broads, which are, however, kept partially clear by cutting. Heron's Carr, a very finely developed swamp carr to the south-west of Barton Broad was next visited. It contains very finely developed ferns, *Osmunda regalis*, *Athyrium Filix-fœmina*, etc.: the abundance of *Iris Pseudacorus* (which does not flower) is also characteristic, and species of *Ribes* are abundant. Fen carr was observed in process of forming on the outskirts of Heron's Carr. The fen itself is of the Bure valley type and societies of *Sphagnum* and *Drosera intermedia* occur here and there.

Owing to the kindness of Mr. Robert Gurney some of the party were accommodated at his laboratory on Sutton Broad, and the whole party were entertained to tea there by Mrs. Gurney and himself. Mr. Gurney also generously offered to put the whole party up at his laboratory, house, and cottages, but it was not necessary to trespass on his kindness so far, as accommodation was available in Sutton village.

On the morning of August 5th the party travelled to Potter Heigham on the Thurne and inspected a small development of "Hochmoor" with *Sphagnum*, *Polytrichum commune*, *Eriophorum angustifolium*, *Calluna vulgaris*, *Erica Tetralix*, *Drosera rotundifolia*, etc. on the edge of the fen. The party afterwards embarked on a motor-launch at Heigham Bridge and ascended the River Thurne, turning up Candle Dyke to Heigham Sound, with its fine marginal reedswamps dominated by *Typha angustifolia*, and Hickling Broad. *Naias marina* was gathered from its only recorded locality in the British Isles, and then the launch proceeded up the Meadow Dyke to Horsey Mere, stopping on the way to visit Blackfleet Broad, now a small patch of water almost isolated in the fen. The fen surrounding this broad interested the party considerably. It is of brackish type with *Œnanthe Lachenalii*, etc. *Lastrea cristata* occurs here as well as societies of *Sphagnum* on tussocks of *Phragmites*. In Horsey Mere itself *Lychnothamnus stelliger* was gathered. The water of the whole of this series of broads is more or less brackish, and has an interesting plankton very poor in species but containing some marine or brackish water Diatoms, while such plants as *Cochlearia officinalis*, *Plantago maritima*, *Scirpus maritimus* and *Triglochin maritimum* are scattered through the district. After leaving Heigham Sound the launch proceeded down the Thurne into the Bure and up as far as Horning. Opposite the Church the party disembarked to inspect typical Bure Valley fen and well developed fen carr. Then the launch continued to Woodbastwick Old Hall, where Mrs. Barclay entertained the party to tea. Hoveton Great Broad was then visited in boats in company with Mrs. Barclay, and an attempt was made to enter a small broad connected with the Great Broad where swamp carr is very finely developed in connexion with tussock swamp of *Carex paniculata* and *C. acutiformis*, but owing to the shallowness of the water and to the fact that very little time was available the attempt had to be abandoned. The launch then continued to Wroxham, past the abundant carrs developed on the fenland of this region of the Bure valley. The train was then taken to Cromer, and after supper, the party proceeded to Holt, where the night was spent.

On Sunday, August 6th the day was spent among the maritime formations of Blakeney Harbour, under the guidance of Professor F. W. Oliver. The main feature of interest here is the great shingle bank which stretches for miles along the coast and protects the estuary of the Glaven (Blakeney Harbour) in which salt-marsh vegetation has developed. Lateral shingle beaches stretch landward from the main bank, and represent successive inwardly turned terminations of the main bank, which has gradually extended westwards along the coast. In the bays enclosed by these lateral banks successive stages in the development of salt-marsh formation, from the open association of *Salicornia europæa* with unrooted *Pelvetia canaliculata* to the general salt-marsh association. On the shingle beach itself *Suæda fruticosa*, which often forms dense thickets two feet or more high, flourishes abundantly. This is apparently its most northernly station in the British Isles. *Arenaria peploides*, *Silene maritima* and *Rumex crispus* var. *trigranulatus* are the other plants which are most abundant on the shingle-beach, while *Mertensia maritima*, the Oyster-plant, with its fleshy leaves simulating pebbles here occurs at the southern extremity of its range on the east coast. *Limonium bellidifolium* (*Statice reticulata*) occurs where mud has been deposited on the shingle and *Limonium binervosum* in other places. Sand dunes have accumulated in places on the top of the shingle, and the process of the formation of these by the accumulation of sand round seedling plants of *Ammophila arenaria* can be observed. After lunch at Blakeney Point, the party sailed across on the high tide to Blakeney, and drove from there to Morston. From here Stiffkey salt-marshes and "meols" (sand dunes) were visited on foot, and the associations of *Glyceria maritima* and *Juncus maritimus* (later developments of the salt-marsh formation not to be observed in Blakeney Harbour itself) were observed. A bəautiful example of the gradual destruction of the *Glyceria*-association by wave erosion occurs here. In the evening the party drove back to Holt.

On Monday morning, August 7th, the party travelled from Holt to Derbyshire, obtaining a good idea of the general features of East Anglia and the Midlands *en route*. The railway passed at first over the varied, generally light soils overlying the chalk of West Norfolk and then across the drained and cultivated Marshland and Fenland south of the Wash. At Peterborough the Fenland was left and the rolling Jurassic clays of the east Midlands with their abundant pasture, now much browned by the long drought, and occasional oak-hazel woods, entered upon. Changing at Leicester much the same type of country, in the valleys of the Trent and its tributaries, was passed through, till the great *massif* of the Southern Pennines was entered near Belper. Along the course of the Derwent valley the Mountain limestone lay to the west, and the siliceous rocks of the Coal Measures and Millstone Grit with extensive areas of moorland to the east. At Miller's Dale station the party alighted and drove to Litton on the limestone plateau, walking thence down Cressbrook Dale to Monsal Dale under the guidance of Dr. Moss. In Cressbrook Dale limestone pasture, limestone scrub and ashwood were successively passed through, and much discussion took place as to the true relationships and *status* of these communities. On the limestone screes were extensive sheets of *Convallaria majalis*. After tea at Monsal Dale, the party drove to Miller's Dale station, and took train to Manchester.

The next three nights were spent at the Midland Hotel, Manchester, where the party was joined by Professor Graebner.

On August 8th a traverse across the moors from Crowden to Greenfield was made. The sides of Crowden Great Clough were covered by siliceous grassland with much *Pteris aquilina*, and a few trees of *Quercus sessiliflora*, *Betula tomentosa* and *Pyrus Aucuparia* in the lateral valleys. The edge of the moors which occupy the peat-covered plateau is very sharp. Blackchew Head moor is largely covered with an association of *Eriophorum vaginatum*, but a good deal of it is much cut up by channels through the peat, and on the drying hags is abundant *Vaccinium Myrtillus*, *Empetrum nigrum* and sheets of *Rubus Chamæmorus*. An extensive new reservoir is being made at the head of Chewbrook Clough and a considerable extent of the valley is devastated. In the evening the party was entertained to dinner at the Midland Hotel by Professor Weiss and Professor Lang.

August 9th was devoted to an excursion to the moors and woods lying to the south of Huddersfield. Owing to the kind offices of Dr. Woodhead some of the members of "the Cave," the oldest club in Huddersfield, generously lent several motor cars for the use of the party, and in this way a great deal of ground was covered most comfortably on this, the hottest day of a memorable summer. The party was met at Greenfield station by the cars and taken at once up over Saddleworth moor, very typical moor of *Eriophorum vaginatum*, so characteristic of the Pennine plateaux. The peat was now exceptionally dry and cracked in many places. Some interesting peat-sections with buried birch were examined, and again the siliceous pasture of the valley sides with continuous belts of *Pteris*, especially towards their upper edges were seen to stand out clearly against the peat-covered plateaux. The cars then proceeded to Honley where the party were most graciously entertained at lunch by Miss Siddon. After lunch Honley Woods of *Quercus sessiliflora* accompanied by Birch with an undergrowth of *Calluna*, *Vaccinium Myrtillus*, *Deschampsia flexuosa*, etc., passing into *Calluna* heath were visited, and afterwards Hey Wood and Woodsome Woods, with the ground vegetation (on the Lower Coal Measures) mainly composed of *Holcus mollis*, *Pteris aquilina* and *Scilla non-scripta*, except in the damper places where there is a more varied vegetation. At Woodsome Wood the party were given tea by Mrs. Woodhead, and afterwards visited Woodsome Hall by permission of Lord Dartmouth, whose agent kindly opened it for the purpose of showing the members of the party the beautiful old court and hall and Renaissance terrace. From Woodsome Hall the party quickly reached Huddersfield, where they were entertained at dinner by the President and members of "the Cave" at a local hotel. The warm-hearted hospitality of their Huddersfield hosts will always be remembered with special pleasure of the party.

On the morning of August 10th the party left Manchester for Southport and Ainsdale to visit the extensive Lancashire sand dunes under the leadership of Professor Weiss and Mr. Ball (of

Southport). From Ainsdale the members walked down to the seashore and along the front of the dunes, where the association of *Agropyron junceum* on the low dunes was inspected. Very few genuine strand-plants occur, this association being represented almost solely by *Salsola Kali*. Passing across the frequently wind-eroded *Ammophila*-dunes behind, the party entered the region of the "slacks" or dune valleys, the extensive development of which is a characteristic feature of these dunes. *Salix repens* is a striking feature of the slacks and accumulates numerous secondary dunes. The slacks were bright with the large flowers of *Parnassia palustris*, and *Pyrola rotundifolia* was abundant in the drier examples of the association of *Salix repens*. Many interesting plants were found in the slacks, but unfortunately the drought had caused the temporary disappearance of many of the interesting Bryophytes, and in the absence of Mr. Wheldon, who was to have joined the party, but was unfortunately prevented from doing so, little was seen of the particularly interesting Bryophyte vegetation of the dune slacks. *Viola Curtisii*, and several forms of *Œnothera* were found near Birkdale. In the evening the party proceeded by train to Preston and Lancaster, where they were met by Mr. W. M. Rankin, under whose guidance the next two days were spent.

August 11th was spent in the limestone district of Silverdale, where much of the country is covered with ash-oak wood. In the basin of the old "Burton Lake," now long since vanished, the lowland moor developed on peat was visited. The peat has been extensively removed and little or no untouched moor is left, but various stages of the recolonisation of the peat-bog vegetation were observed. An excellent peat section, which Mr. Rankin had specially re-dug for the benefit of the party, was examined. The section showed a very interesting succession of vegetation. "Moor peat" composed of *Sphagnum*, *Eriophorum* and *Calluna* was underlaid by a layer of birch *in situ*, and this by peat composed of the remains of *Cladium* and *Phragmites*. Below the sedge-peat a layer of *Hypnum*, and then of amorphous peat, rested on shell marl, evidently deposited on the floor of the ancient lake. The whole sequence told the story of the obliteration of the lake by fen, the growth of a birchwood upon the fen, and the subsequent destruction of the wood by a *Sphagnum*-bog. The succession is strikingly similar to those described by Weber and other continental authorities on peat. The party afterwards visited Haweswater, a small existing lake with good reedswamp on the sheltered side, and bare banks where they are exposed to wind and wave action. Adjoining the lake is limestone bog with *Primula farinosa*, *Selaginella selaginoides*, etc. Some of the party examined a salt-marsh near Arnside, which Professor Oliver reported as exhibiting very interesting features. Lancaster Castle was visited in the evening by special permission of the Constable.

On August 12th the party travelled to Grange and drove to Foulshaw Moss, a comparatively untouched lowland moor with an existing vegetation of *Eriophorum vaginatum*, mixed with *Scirpus cæspitosus*, over most of its extent. There is historical evidence that this "moss" was comparatively recently much wetter than it now is, and no doubt largely occupied by *Sphagnum*. The drying of the moss still continues, but is largely aided by peat cutting; the parts most affected bear a mixture of *Eriophorum* and *Calluna* and are eventually colonised by birch and Scots pine from neighbouring woods and plantations. Thus by the time the *Eriophorum* has disappeared regular birchwood is formed, with pine, mountain ash, yew, sallows, etc., and in places a ground vegetation of *Molinia Vaccinium*, etc. The wetter parts of the moor are still occupied by *Sphagnum*-bog. Sections of the peat show a very similar sequence to that of the "Burton Lake" peat, except that the upper *Sphagnum*-peat passes up into a thin layer of *Eriophorum*-peat on which grows the existing Eriophoretum, while below, the fen peat is separated from the *Sphagnum*-peat by birch and pine *in situ* and is based on an estuarine silt containing the roots of trees. Here then we have two complete successions, that of the fen and that of the moor, each culminating in a wood-association, while the remains of a very ancient wood destroyed by the growth of the fen is found at the extreme base. The remains of an ancient "corduroy road" consisting of logs placed transversely occur in the midst of the *Sphagnum*-peat. Mr. Rankin's excellent work on these lowland moors was the subject of general congratulation. A brief account appears in *Types of British Vegetation*, but it is to be hoped that a fuller account will shortly be published. The party afterwards visited the gardens of Levens Hall with its famons topiary work, and in the evening travelled from Oxenholme to Penrith, where they were met by Dr. F. J. Lewis.

On Sunday, August 13th, an early start was made for Crossfell, the party driving to Kirkland at the foot of the mountain. The Crossfell ridge consists of alternating bands of gently inclined limestones, flags and grits. The western escarpment is formed of a series of terraces, the steps being formed of limestone, free from peat, and covered by a thin soil forming typical limestone grassland with *Festuca ovina*, *Sesleria cærulea*, *Agrostis vulgaris*, *Kœleria cristata*, *Poa pratensis*, and various "calcicole" plants. The sandstones and flags form slightly inclined platforms between the steps, and are covered with siliceous grassland, largely dominated by *Nardus stricta* and *Juncus squarrosus*, with stunted moor plants such as *Calluna*, *Vaccinium Myrtillus*, etc., in places where there is a distinct accumulation of peat. On the western side of Cross Fell itself there is no extensive moorland association, but on adjoining parts of the ridge, moor comes down to an altitude of about 600 metres. Dr. Lewis is, however, of opinion that the whole western face of the range was at one time covered with peat, that the local patches of peat on the western side of Cross Fell are the remains of this extensive mantle, and that the cause of its disappearance is probably to be found in the increasing dryness of the climate. He sees evidence for this view in the widespread degeneration of the moor formation throughout the British Isles, as shown by the occurrence of "retrogressive moor" (a term due to Dr. Moss, who does not, however, assign its origin to a change of climate) on many high plateaux. This retrogressive moor is characterised by the erosion of the peat and by the constant occurrence of *Vaccinium Myrtillus*, *Empetrum nigrum* and *Rubus Chamæmorus* on the hags between the erosion channels. The association occurs on the hills adjoining Cross Fell itself and on the undulating plateau lying to the east. Other moor associations represented in this area are Eriophoro-Callunetum, a frequent transition, on the Pennines, between cottongrass moor and heather moor, and pure cottongrass moor, here characterised by dominance of *Eriophorum angustifolium*, in place of *E. vaginatum*, the dominant of the typical cottongrass moors of the Southern Pennines.

After ascending to the summit of Cross Fell, which is occupied by a small area of alpine plateau characterised by weathered hummocks of *Rhacomitrium lanuginosum* and by the presence of *Carex rigida*, but, in general, extremely bare of plants, alpine or otherwise, the party traversed the eastern moorland as far as the Lambgreen Hills, which form abrupt slopes of drift limestone rising out of the moorland. The contrast between the limestone grassland of these slopes and the adjacent moor association is very sharp and striking. One can literally step from one to the other. The peat of the moor close to the Lambgreens is extensively denuded and in the stretches of bare peat between the hags the remains of a regular birch forest are exposed, the white bases of the trunks and spreading roots forming a striking feature. This old birch forest is at an altitude of over 2,000 feet (600 metres). The bareness of the peat in this region is attributed by Dr. Lewis to denudation, but Professor Graebner was of opinion that it was due to a "bog-burst." In the evening the party drove back to Penrith, where the night was spent.

On August 14th the train was taken to Carlisle and thence by the North British route, *viâ* Hawick, to Edinburgh. This route gives an excellent general idea of the Southern Uplands of Scotland and very careful descriptive notes had been prepared by Dr. W. G. Smith. The extraordinary poverty in natural or semi-natural woodland, sufficiently marked in much of northern England, is even more striking in this traverse of the Southern Uplands. Edinburgh was reached at 3 o'clock, and shortly afterwards the party visited the Royal Botanic Gardens by invitation of Professor Bayley Balfour, who conducted the party through most of the Gardens and houses. The alpine department and the cultivation of the heaths were much admired. In the evening Professor Balfour entertained the whole party to dinner at Inverleith House, where haggis and grouse formed part of the *mênu*.

The morning of August 15th was spent in visiting Edinburgh Castle and other places of interest in the city, and in the afternoon the party left for Dunkeld. Dr. Smith again supplied careful notes on the route. At Perth, which was reached at 3.23, the Museum was visited and the collections inspected, including a collection of Scottish arctic-alpine plants specially selected for the occasion. Perth was left at 7.15 and Dunkeld reached at 7.42. In the evening a Highland piper entertained the party, but the music of the pipes was not equally appreciated by all the members.

On August 16th a half-day was spent round the lochs and in the woods north of Dunkeld. The woodlands included examples of good typical wood of *Quercus sessiliflora*, but much has been replanted at different periods. Round Cally Loch are many exotic deciduous trees, while in the Loch itself *Aponogeton* and *Nymphœa candida* grow profusely. In the older plantations of Scots Pine, tall clumps of Juniper were conspicuous in open parts, while the usual ground vegetation on dry humus included, with *Calluna*, *Vaccinium*, etc., *Trientalis europœa*, so characteristic of old woods in this district. Further off on the hills were seen the woods of Larch extensively planted on the Atholl estate over 100 years ago. On the lochs special facilities were granted by the Marquis of Tullibardine; boats were available and some members examined the aquatic vegetation of these lochs of the "Highland" type. *Lobelia Dortmanna* was abundant, while *Isoëtes lacustris*, *Naias flexilis* and other representative species were collected. On the shores of Butterston Loch the party passed through a swamp of *Alnus* with *Myrica* and *Juniperus*, fringed on the landward side by abundant *Rosa spinosissima*. The grounds of Dunkeld House were afterwards visited and the party were photographed round the stump of the oldest larch in the British Isles which was planted in 1738, shortly after the introduction of the tree and was killed by lightning in 1906; it clearly shows more than 160 rings. Dunkeld and its neighbourhood possess a large number of interesting exotic conifers many of which were planted shortly after their introduction to Europe, and these greatly interested the foreign visitors. In the afternoon the party travelled from Dunkeld to Aberfeldy and drove thence to Fearnan and Lawers village, on Loch Tay, where the night was spent.

The following day, August 17th, the ascent of Ben Lawers was made, the party being joined by Professor Bayley Balfour, who had travelled from Edinburgh for the purpose. The route by the Carie Burn was taken, and the following zones of vegetation were recognised, following Dr. W. G. Smith's recent account in *Types of British Vegetation*. First the enclosed pastures whose vegetation has been influenced by the manuring incidental to pasturage, extending from Loch Tay to a height of about 1,000 feet; then unenclosed sheep pastures extending as far as the first ridge of moraines (1,500—1,750 feet) and dotted with heather in places. The unenclosed pasture passes, on the flat undulating ground between the low ridge and Lawers itself, into the grass-moor, which is dominated by *Nardus stricta* and *Juncus squarrosus* on peat. The grass-moor runs a considerable distance up the slope of Ben Lawers itself and at a height of about 2,250 or 2,500 feet gives place to the first strictly arctic-alpine association, dominated by *Alchemilla alpina* and various grasses, such as *Festuca ovina*, *F. rubra*, and *F. vivipara*, *Deschampsia flexuosa*, and forms of *Poa alpina* ((2,500–3,500 feet). This is apparently the culminating association on well drained talus slopes. Above this we came to the arctic-alpine chomophyte associations of the ledges and fissures of the corries south-west of the summit, which were reached by leaving the course of the burn and striking obliquely up the slopes covered by the *Alchemilla alpina* association. Above the corries the summit plateau is covered by the plant-formation of mountain-top detritus in which mosses and lichens, and notably *Rhacomitrium lanuginosum*, are the pioneer and, in the more exposed places, always the leading plants. The Swiss botanists recognised in those black crusted tracts and patches so characteristic of the summit region, the "schneetälchen" of

Switzerland, with the liverwort *Anthelia Juratzkana* forming the first coloniser of the snow-washed soil, accompanied by the characteristic *Gnaphalium supinum*, and the orange lichen *Solorina crocea*. The "*Saxifraga cernua* corrie" proved most interesting and during the descent Professor Balfour pointed out an extensive association of *Juncus trifidus* competing with the intruding *Alchemilla alpina* pasture association. The more interesting arctic-alpine species, of which a considerable number were found in flower, will be alluded to in Mr. Druce's account of the floristic results of the expedition. After reaching the summit most of the party explored the cliffs above Lochan 'a Chat, and crossed the extensive and partially denuded peat-deposits to the east of the summit, gathering *Cornus suecica* in the *Vaccinium Myrtillus-Empetrum nigrum* association at about 3,000 feet. The whole party met at the Lawers Hotel for tea between 5 and 6 o'clock. Professor Massart obtained a number of excellent photographs of the arctic-alpine associations.

On August 18th the early steamer took the party to Killin pier and thence by train through Glen Ogil and by Loch Earn to Callander. After an early lunch the party drove to the Trossachs, and after walking a little way along the shores of Loch Katrine, turned back through the wood to Loch Achray. This wood proved to be a very beautiful and typical example of a *Quercus sessiliflora* wood with heathy ground vegetation, a type so common on the old siliceous rocks of northern and western Britain. A few plants belonging to the non-heathy type, e.g., *Scilla non-scripta*, occurred here and there. On the cliffs to the north the characteristic zonation of oak below and birch above was well seen. The party returned to Callander, where the night was spent.

On the morning of August 19th the party travelled to Glasgow, and after a brief view of the Town Hall, etc., went straight to the Botanic Garden, where Dr. Lawson kindly showed the well-known moss-house. The Botanical Institute was afterwards visited, and then Professor Bower, who was not fully recovered from a sprained knee and came over from his house on crutches, entertained the party to lunch at the Students' Union. The afternoon was spent at the Glasgow Exhibition where the historical and particularly the "prehistorical" section greatly interested the party. In the evening the party left for Greenock where they embarked for Dublin.

On the morning of Sunday, August 20th, after a smooth passage, the party arrived in Dublin and were met on the quay by Mr. Lloyd Praeger, who had organised with his usual care and thoroughness the Irish portion of the tour, and who acted as guide throughout Ireland. The Botanic Garden of Trinity College was visited in the forenoon under the guidance of Professor H. H. Dixon, while in the afternoon the Glasnevin Gardens were visited by most of the party, a few members going instead to the sand dunes and salt marshes of the North Bull.

On August 21st the party left Broadstone station by the westbound mail at 7 a.m., and travelled right across Ireland to Clifden, Co. Galway, where the afternoon was spent on the hillsides on the north of Clifden Bay. The constant association of *Ulex Gallii*, *Dabeocia polifolia* and *Erica cinerea* in clumps scattered in the grassland was the most striking vegetational feature. Several interesting western plants were found. The magnificent roadside bushes of *Fuchsia Riccartoni* (quite naturalised and said to reproduce itself from seed, though no undoubted self-sown seedlings were seen in the neighbourhood of Clifden) were much admired. In the evening the small laboratory of the Irish Department of Agriculture, in which much good work on the diseases and manuringof the local crops is being done by Dr. G. H. Pethybridge and his assistant, was visited.

On August 22nd cars were taken to Craigga More. *Eriocaulon septangulare*, the most abundant of the American plants found in West Ireland, was seen in abundance in several roadside pools. Near Craigga More Lough plenty of *Erica Mackaii* was found, replacing *Erica Tetralix*, and on the islands in the lough the dwarf woods sheltering a woodland vegetation were visited (see NEW PHYTOLOGIST, Vol. VIII, pp. 253-5), while other members of the party cursorily examined the adjacent moors. The drive was then continued to Roundstone, whence, after a meal, Urrisbeg was ascended; from the top a splendid view is obtained of the surrounding country: on the north the typical Connemara moors, studded with innumerable lakelets and with the rounded summits of the Twelve Beinns behind, on the east the greatly indented inlets of Roundstone Bay with their seaweed-covered rocks running far up into the moorland; to the south the characteristic limestone hills of the Burren in Co. Clare across the broad expanse of Galway Bay. An interesting discussion on the geology of this district, which has been entirely and strongly glaciated, and on the origin of the peat-covering, took place on the summit of the hill. *Ulex Gallii*, again associated with *Dabeocia* and *Erica cinerea* was particularly finely in flower on Urrisbeg, which like the shores of Clifden Bay is marked by alternation of heath with grassland. *Spiranthes autumnalis* was abundant in the turf. The party then descended the hill on the south side and visited the much denuded sand dunes of Dog's Bay. These furnish a capital example of degeneration of a habitat. The dunes have passed through the stage of fixed dune grassland, of which some few tracts still remain, with *Eryngium maritimum* and *Euphrasia curta*, but most of the turf has been destroyed and bare sand remains. Here and there small dunes are being slightly regenerated, through the agency of such plants as *Carex arenaria*, *Agropyron junceum*, and, in places, *Potentilla anserina*. *Ammophila* is very scanty and what there is seems to have remained from an earlier period when the dunes were in a primary phase of development. *Salsola Kali*, *Arenaria peploides*, *Polygonum Raii* and *Spergularia rupestris* occur on the shore. From Dog's Bay the party drove back to Clifden in the evening, passing many typical Connemara cottages and villages, with marsh and moor plants springing up in the middle of the miserable crops of oats and potatoes, which are often sown in scarcely drained moor. The extreme poverty of this part of the country made a deep impression on the American visitors.

On the morning of the 23rd the early train was taken to Galway where a good deal of time had to be spent on account of the delay in the departure of the steamer to Ballyvaghan, which was not reached till about 4 p.m. The party were met on the quay by cars and drove at once in the direction of Black Head. Owing to the lateness of the hour the cars were stopped about halfway and the party climbed the hillside and examined the vegetation of the limestone slopes, terraces and pavements, till the fall of dusk made it impossible to continue. One centre of interest was the occurrence of heath plants on the limestone. *Calluna vulgaris*, for instance, grows vigorously, with living functional roots pressed against the surface of the limestone rock. The ling does not, however, grow alone in this position, but always in the midst of great clumps of mosses, in the humus formed by which its seedlings have probably germinated. There is a very extensive heath flora, which specially interested Professor Graebner, on these limestone terraces. The other point of interest was the vegetation of the limestone pavements and particularly of the great chemically eroded fissures which abound in them. Here many species of trees and shrubs grow luxuriantly, but very seldom project above the surface of the pavement. It was generally agreed that this Burren country, with its almost untouched vegetation presenting an abundance of problems, deserves very thorough ecological study, which could only be carried out by carefully planned co-operative work with a properly equipped field station. When dusk fell the party returned to the road and drove back to Ballyvaghan in a nearly saturated atmosphere which foretold a change in the weather. Heavy rain, the first (except for a few drops at Blakeney) that had been experienced during the tour, fell during the night, and for the remainder of the time spent in Ireland the weather was unsettled and wet.

On the morning of August 24th some of the party visited before breakfast a fine area of *Potentilla fruticosa*, which is locally abundant in this region. After breakfast cars were taken for the drive to Ardrahan, entirely through the limestone country, with its regularly terraced hills and intervening stretches of plain. One of the most remarkable features of this highly glaciated region is the great scarcity of drift: where drift does occur it is at once recognisable by its different contours and the different vegetation which it bears. A short stop was made on the way to look at another piece of limestone pavement, but heavy rain drove the party back to the cars. After lunch at Ardrahan the train was taken for Limerick, Mallow and Killarney, which was reached late in the evening.

On August 25th the party drove to the Upper Lake, where the morning was spent in the woods on the Old Red Sandstone dominated by *Quercus sessiliflora*, with *Ilex Aquifolium* specially abundant, and yew, birch, mountain ash and *Salix cinerea*. Besides the ground flora characteristic of *Quercus sessiliflora* woods, *Saxifraga umbrosa* and *Euphorbia hiberna* were conspicuous and abundant, and *Melampyrum pratense* var. *hians* with its bright golden flowers and distinctly open palate was a beautiful feature. But the most interesting plant of all was, of course, *Arbutus Unedo*, which in spite of much destruction in past times is still abundant and locally dominant in these woods. The great luxuriance of all the plants, the abundance of bryophytes and of plants growing epiphytically on the trees, especially *Polypodium vulgare* and *Saxifraga umbrosa*, were a distinctive feature of the vegetation. *Pinguicula grandiflora* was gathered near the present upper limit of the woods, but *Saxifraga Geum* was not seen nor was the "Killarney Fern" (*Trichomanes* *radicans*) which is now excessively rare. The weather was close, warm and "muggy" with an overcast sky and occasional drizzling rain, as if to give the visitors a correct impression of the climate determining the typical south-western vegetation. The Lower Lake was reached by boats on the return and a list was made of the plants on a wooded limestone island; from the dominance of ash, the much greater variety of shrubs, some of which are characteristic limestone species and the absence of *Calluna*, etc., it was clear that the difference of soil has its usual effect in this region in spite of the very strongly marked climate.

On August 26th the party travelled to Cork and visited the garden of Mr. Beamish at Ashbourne, near Queenstown Junction. In spite of the nearly continuous rain the members of the party, under the delightful guidance of their enthusiastic host, were keenly interested in the immense variety of plants which Mr. Beamish has got together in an incredibly short time. The rock garden, originally made in an old quarry, is specially rich and beautiful. Mr. and Mrs. Beamish afterwards hospitably entertained the party to lunch, and an unwilling departure was made in the afternoon in order to catch the steamer from Cork for Plymouth.

August 27th. The rugged cliffs of the Land's End, shrouded in mist, were sighted early in the morning after a fair passage, and most of the day was occupied in skirting the Cornish coast, Plymouth being reached about 4 p.m., in grey misty weather. The laboratory of the Marine Biological Association was visited by a few of the party, who were kindly shown round by the Director, Dr. Allen.

On the following morning, August 28th, Plymouth was left by an early train for Cornwall. At Truro most of the luggage was left and the party was joined by Mr. Hamilton Davey, the author of the *Flora of Cornwall*, who kindly accompanied the party during its stay in the county. After changing at Gwinear Road, Helston was reached and a special motor-omnibus taken to Lizard Town. By the roadside *Erica vagans* was soon seen in full flower and on the heaths of the Goonhilly Downs great sheets of it were passed. At Lizard Town the party were met by Mr. P. D. Williams of Lanarth. After lunch the party walked to Kynance Cove across the Lizard Downs, finding a number of characteristic species and the dwarf forms of several others, which are typical of the grassland of these cliffs. Beyond Kynance a wide circle was made over the heathland and some interesting observations were made on the ecological relations of these heaths, a thorough study of which would certainly lead to interesting results. The conclusion was reached that burning certainly has an effect of leading importance, for on a recently burned area all the species which are commonly found were at once returning, mainly by shooting from persistent underground organs, and the power to return quickly and occupy the soil must thus have a determining influence on the actually existing vegetation.

On August 29th most of the party drove *viâ* Mullion, where half-an-hour was spent on the cliffs, to Penrose by kind permission of the owner, and the vegetation of Loo Bar was briefly investigated. Meanwhile two or three of the members visited Mr. Williams' garden at Lanarth and also a hybrid of *Erica vagans* and *E. cinerea* recently discovered by him. Lunch was then taken at Helston, and the party travelled to Truro. From Truro a local train was taken, and this was stopped by the kindness of the Great Western Railway Company on the line near Perranwell, so that the party could get as rapidly as possible to one of the best localities for *Erica ciliaris*. This plant was in splendid flower on a damp heath near the railway in conjunction with *Ulex Gallii*, *Erica Tetralix*, *Molinia cœrulea*, etc. The hybrid *Erica ciliaris* × *Tetralix* was very frequent, associated with the parent species. This area has been recently encroached upon by arable land and is one of those which could be usefully preserved in perpetuity, not only as the habitat of a rare species, but as an example of an association which might easily come to be altogether destroyed. After returning to Truro the party were most hospitably entertained to dinner by members of the Royal Institution of Cornwall, the Bishop of St. Germans presiding. A great deal of trouble was devoted to organising this dinner, especially by Mr. George Penrose, the Secretary of the Royal Institution and Curator of the Truro Museum.

On August 30th the party travelled from Truro to Portsmouth and the peripatetic part of the expedition came to an end. During the week of the meeting of the British Association, however, the members of the party remained together, arrangements having been generously made by the local hospitality committee for their accommodation at two of the hostels belonging to the Women's Training College, and here. as guests of the Mayor, they were most excellently entertained by Miss White the Lady Superintendent and Miss Fawkes the Matron, while Mr. Delahunt the Local Secretary of Section K, was most assiduous in his efforts to provide the visitors with every facility that could be desired. To all concerned in this admirable example of organised hospitality the warmest thanks of all the members of the party are due.

The excursions of Section K, rather more numerous than usual, had been chosen with a view to the needs of the international party, and in addition to these one or two others were arranged apart from the Section. Portsmouth proved an excellent centre for illustrating the vegetation of the south of England, as opposed to that of the north and west of the British Isles, through which the route of the excursion mainly lay.

On the afternoon of Friday, September 1st the party travelled to Chichester and drove to Kingley Vale, five miles to the north-west, where in a dry valley of the chalk there is probably the finest example of a nearly pure yew-wood in the British Isles. Some of the continental visitors, indeed, were of opinion that it is probably the finest example in Europe. On the top of the down above, an excellent example of a heath on clay-with-flints overlying the chalk, with *Ulex nanus*, a characteristic species of the heaths of the central part of southern England, was visited.

Saturday, September 2nd was devoted to an excursion of Section K to Denny Bog and the adjacent parts of the New Forest. The zoned vegetation of the bog, and the adjacent woodland of oak and beech, proved very interesting and many good plants were gathered. The heathland between Beaulieu Road and Lyndhurst Road, on which the Scots pine, said to have been first introduced to the district in 1776, is rapidly spreading, was also traversed.

On Sunday some members of the party visited the salt marshes on the north side of Hayling Island, where Dr. Moss demonstrated various species of *Salicornia*. *Spartina Townsendi* covers large areas of these marshes and *S. stricta* was also found.

In the afternoon of Tuesday, September 5th, an excursion to Southampton Water, under the guidance of Dr. Otto Stapf, who has specially studied these Spartinæ, was made in a steam-launch. Near Warsash, on the Hamble Creek, *Spartina Townsendi*, the supposed hybrid between *S. stricta* and *S. alterniflora*, covers the salt marsh, as it does on nearly all the shores of the Water. A local patch of *S. alterniflora* was also found, but no *S. stricta*. The launch then proceeded up Southampton Water close to the west bank as far as Hythe pier and obtained a good view of the vast stretches of *S. Townsendi* which have covered the mud flats of that shore within recent years. On the return journey the party landed at the point of the Calthrop Castle shingle spit and spent a short time examining the vegetation of this bank, which protects the *Spartina*-marsh behind it.

On Wednesday, September 6th, the last expedition of the tour was made. This was to the chalk downs near Butser Hill and to the woods of Ditcham Park, by invitation of Mr. Cave. The train was taken to Rowland's Castle station on the direct Portsmouth line of the South Western Railway. Here the party were met by Mr. Cave with four motor-cars, and were driven to the "Coach and Horses" on the London road where it rises to cross the chalk downs close to Butser Hill. The dry chalk valleys contain a well developed scrub of many different species of shrubs. The chalk grassland is nibbled exceedingly close by rabbits, which swarm on these downs, and but few plants, of which *Senecio Jacobæa* is the most conspicuous, propagate themselves by seed under these conditions. Ground vegetation is practically non-existent in the fragments of beechwood which remain (*e.g.*, on Holt Down) but the thicker ashwoods and copses are, for some reason, less afflicted by the scourge and have quite an abundant and varied flora. The party crossed Holt Down and passed through woods of mixed beech and ash, with oaks conspicuously absent except where the rain-wash had provided a deeper soil towards the bottom of the valley. On the opposite slope, within the boundary of Ditcham Park, fairly typical oak-hazel copse, developed on a deep relatively non-calcareous soil overlying the chalk was met with. From this point the cars were taken to Ditcham House where Mr. and Mrs. Cave entertained the party to lunch. In the afternoon the typical beechwoods of the chalk escarpment facing the Weald were visited. Here the ground vegetation is much less affected by rabbits, though it is probable that their influence is still felt and may have something to do with the absence of free regeneration of the woods from seed. Afterwards a slope of down crowned by a mixed wood of beech, ash and yew was visited. Here two plots of ground on the edge of the wood and grassland had been enclosed two-and-a-half years ago with rabbit-proof wire fencing, and the effect on the herbage of the down was extremely marked. The protected down grassland was said by the American visitors to resemble closely some types of prairie. The enclosures were made largely with the object of determining if the ravages of the rabbits alone prevented the regeneration of the wood, but no positive results are as yet forthcoming on this point. After tea at Ditcham House the party were driven back to Rowland's Castle and took train to Portsmouth. This excellent and extremely pleasant excursion, which was made possible through the kindness of Mr. and Mrs. Cave, formed a brilliant wind-up to the expedition: on the next day there was a general dispersal of the members of the party.

So far as the carrying out of the programme was concerned, the whole excursion worked very smoothly, thanks mainly to careful organisation beforehand. The people responsible for the different sections of the tour made all the local arrangements for hotels, driving, etc. The General Manager of the Midland Railway made the railway arrangements, the necessary accommodation being in most cases reserved for the party by the different companies. In Ireland there was a reserved double saloon on the Midland and Great Western, and a reserved coach on the Great Southern and Western, while the London and South Western Railway provided a through coach from Exeter to Portsmouth. The party had very great luck in being away from the centres affected by the railway strike during the continuance of the strike. The only hitch that occurred was the loss of some luggage for about a fortnight. It was eventually found and restored to the owners, though with some damage.

The weather was hot and dry throughout, except during three days in Ireland. The health of the party was excellent, scarcely a single member being indisposed during the whole five weeks. In spite of the strenuous nature of the tour everyone was perfectly fit and well at its close, and ready to begin all over again. A more amiable and harmonious party, a set of people easier to deal with, more anxious to be pleased and to make the best of everything, can hardly be imagined. There was absolutely no friction of any kind whatever, and many old friendships have been strengthened and new ones formed.

With regard to the scientific results, floristically the tour was a decided success. The long companionship in the field of continental and British field botanists could not avoid giving to both clearer ideas of critical species, and incidentally several species and varieties new to Britain were discovered. For details Mr. Druce's paper in the next issue of this journal should be consulted. In regard to the conceptions of units of vegetation, opportunities such as these of meeting in the field workers from different countries are, in the opinion of the present writer, absolutely essential to progress in the present position of the subject. The fruits of this particular expedition will become apparent in the future, while the stimulus afforded to the British workers both by the kindly appreciation and by the keen criticism of the visitors, will certainly be very marked.

The organisation of the present excursion has led to a determination on the part of the foreign visitors to organise similar expeditions in their own countries. Professors Clements and Cowles have decided to arrange an international excursion in the States in August and September, 1913; and Professor Schröter, Professor Massart and Dr. Ostenfeld have in view international excursions in Switzerland, Belgium and Denmark in 1915, the year of the International Congress in London, when the American botanists expect to be again in Europe. There was also talk of an International Phytogeographical Society. Such a society, if it were given a suitable organisation, would be of the greatest service in advancing the subject, which is nearly ripe for an effort of this kind.

In the next number of this journal we shall publish an account of the floristic results of the excursion by Mr. G. Claridge Druce, and in succeeding numbers we hope to publish some impressions from the foreign visitors.

A. G. TANSLEY.

NOTES ON RECENT LITERATURE.

The Cambridge Manuals of Science and Literature.

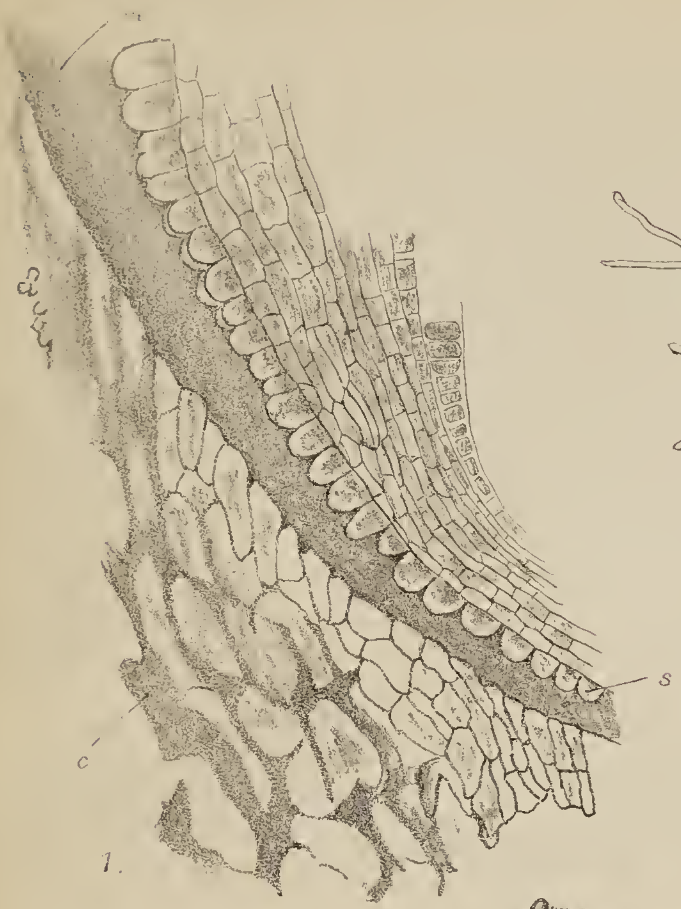
SINCE the last notice in these pages a year ago (Vol IX, p. 340) several volumes of this excellent series have been published by the Cambridge University Press. An interesting note in the *Botanical Gazette*, by Professor Coulter, has recently appeared calling attention to the constant efforts by leading scientific men in this country which have for long been characteristic of English science, to popularise the results of research, and instancing this, together with other shilling series which have lately been established, Mr. E. A. Newell Arber in *The Natural History of Coal* (pp. X + 163) gives what seems an excellent summary account of his subject. The bulk of the book is naturally devoted to the vexed question of origin, and the author concludes that the rival theories are by no means necessarily mutually exclusive. "If we admit that some coals have originated under terrestrial conditions like modern Peats, while others have been formed in estuarine and lacustrine environments, it is hardly possible, in view of the processes of nature which may be studied in progress to-day, to deny that in some cases coals have been formed *in situ*, while in others the mother substance was transported from a distance to the present site of the seam. There is also very little doubt that some coals have been formed partly from drifted material and partly from vegetation which grew in place. Further, in some cases at least, the products which result may be similar, though in one case the mode of accumulation of the mother-substance may have been terrestrial, and in another estuarine." (pp. 148-149).

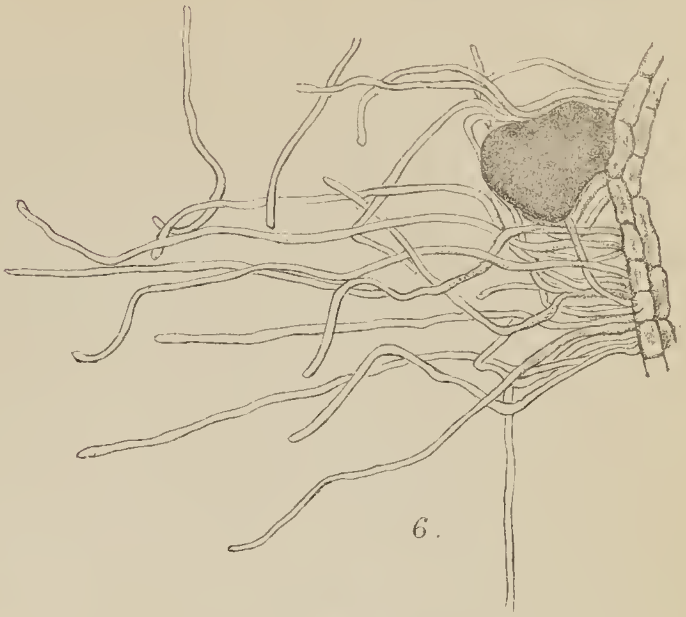
In *Plant-Life on Land: considered in some of its biological aspects* (pp. 172), Professor F. O. Bower strings together a series of loosely connected chapters on various topics which come without any difficulty under his very comprehensive title. The first chapter—"Present-Day Botany—a Contrast" is interesting as containing the first published discussion of the popular misconception of the occupations and range of knowledge of most modern botanists that the reviewer has met with. "Which of us has not been assumed to know at once by sight and to be able to name the various Conifers growing in the plantations round some country house... The assumption is complimentary, but it is apt to be embarrassing... When one is found at fault in the specific distinctions of *Abies* or *Cupressus*, there is some risk of attainments in other branches being unduly discounted. Such knowledge is doubtless desirable, as is all knowledge: but to the majority it would be so much mental ballast . . ." And the author goes on to give some very wise and judicious remarks on the relation of modern specialism to general scientific culture. This is one of the most "readable" of the recently published shilling books on botany, and strikes one as better adapted than some of them to appeal to the plain man.

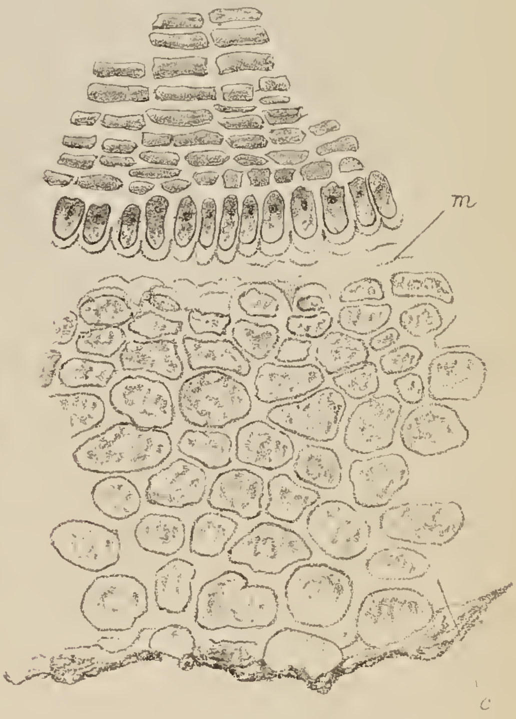
Professor Seward in *Links with the Past in the Plant World* (pp. X + 142) writes attractively of the Longevity of Trees, of the Origin of the British Flora, and then of the Geological Record and of typical existing examples of ancient stocks which connect with the great dominant groups of plants of the remote past.

A. G. T.

R. Madley, Printer, 151, Whitfield Street, W.







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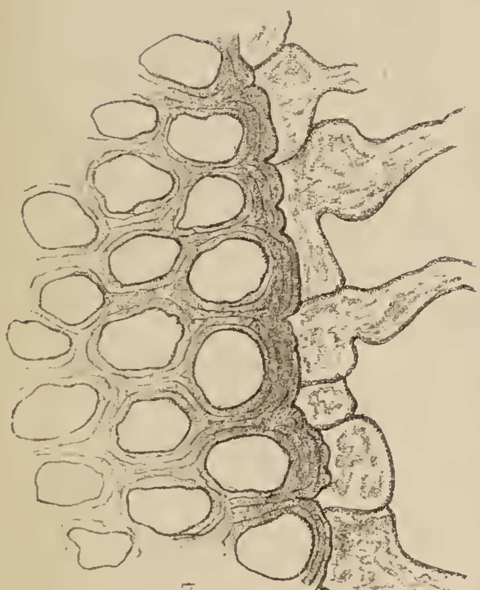
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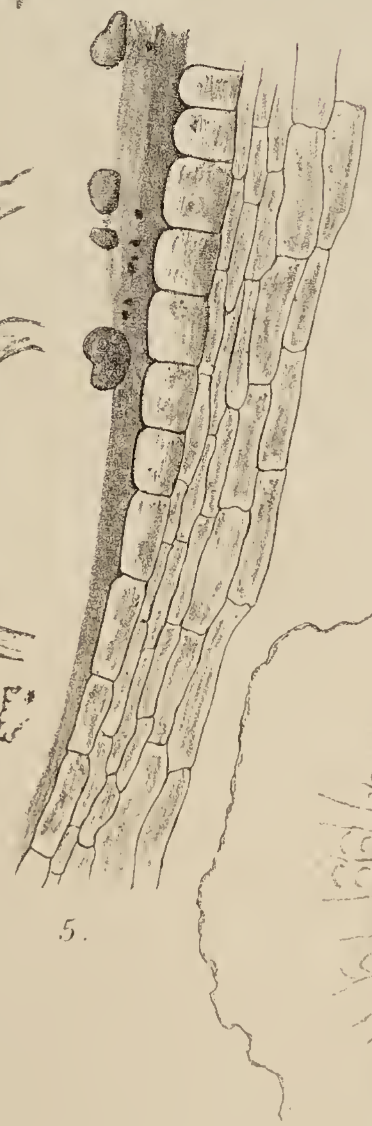
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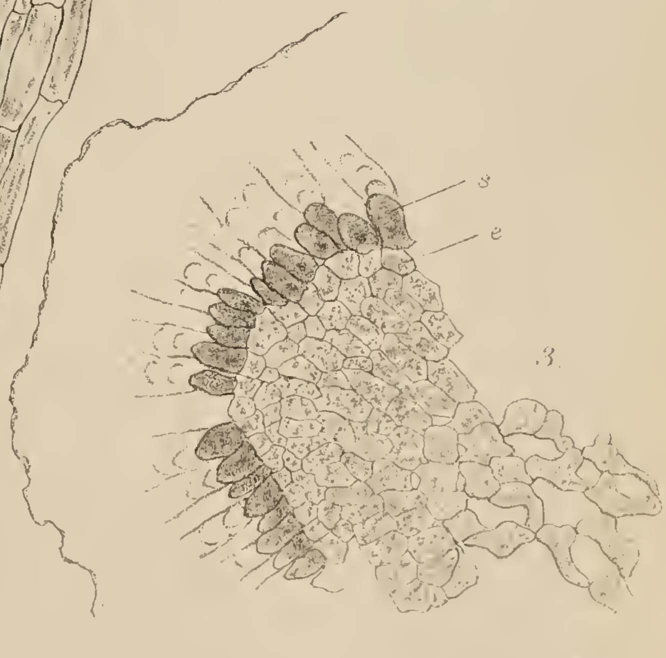

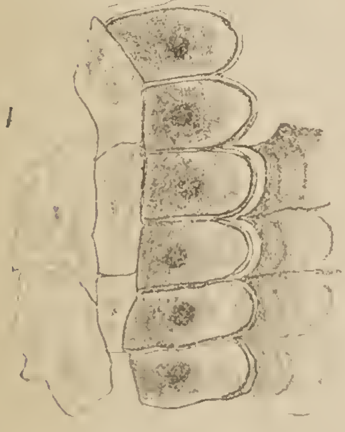

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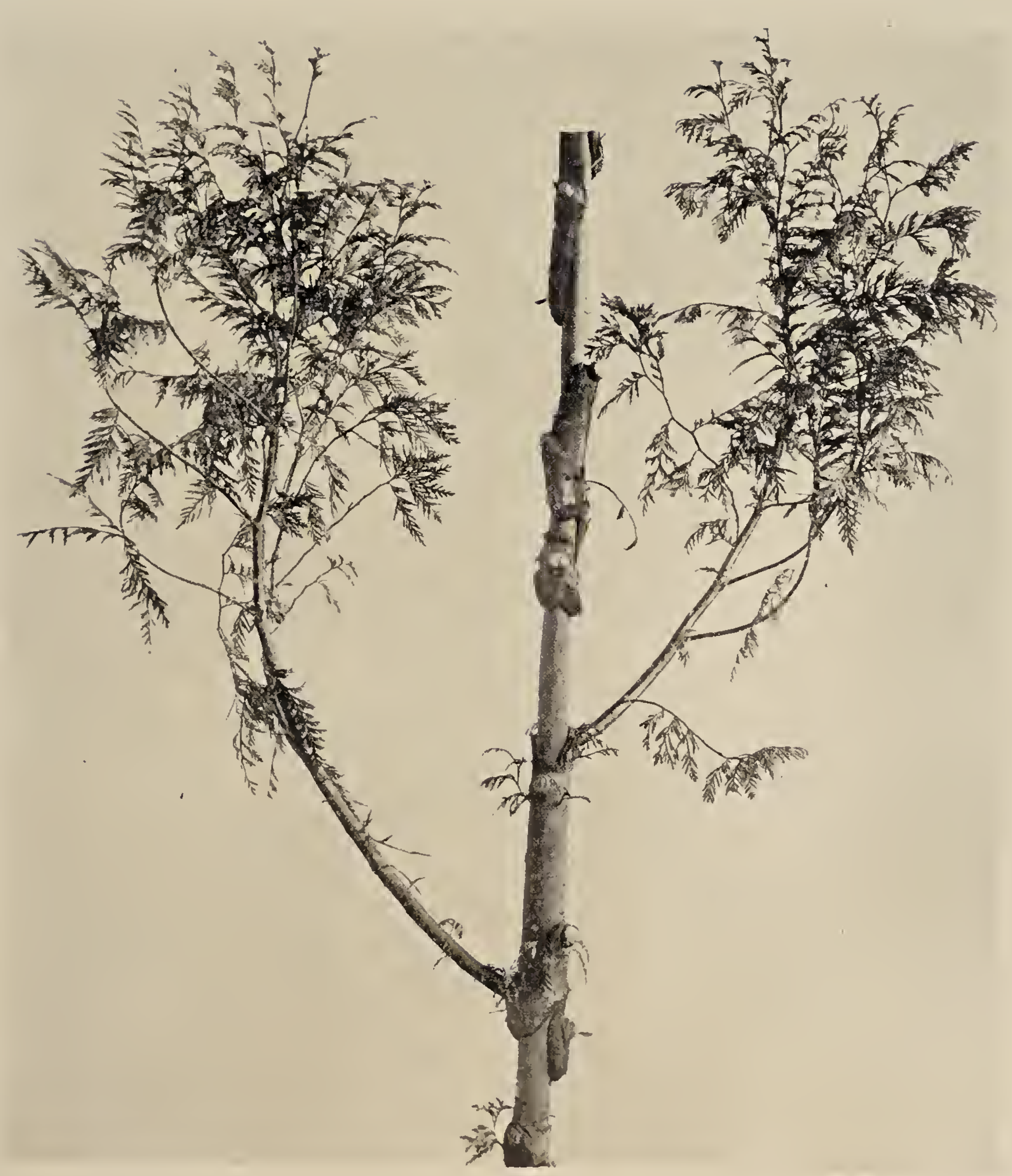

A. W. HILL—*THUYA PLICATA*

DAMAGED BY SQUIRRELS.

THE

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FLORAL EVOLUTION: WITH PARTICULAR REFERENCE TO THE SYMPETALOUS DICOTYLEDONS.

By H. F. WERNHAM.

V. TETRACYCLIDÆ: PART II. TUBIFLORÆ.

WE now approach the study of what is in some respects a remarkably natural group, the key-note of which is zygomorphy, of the kind independent of close aggregation of flowers (*supra*, p. 81). This zygomorphy is coupled with a tendency, fully realized in the majority of the forms concerned, to oligomery of the andrœcium—a secondary economy tendency, following more or less directly upon the bilateral symmetry of the flower. The *primary* economy tendency is thus completely realized in this group as in the Contortæ,—at least, in so far as sporophyll numbers are concerned; while a material and essential advance upon the latter cohort has been made in the direction of general adaptation to the reception of insect-visitors.

We shall meet, however, with an extensive primary economy tendency in respect of the megasporangia, the ovules being constantly two, only, per sporophyll in over 40% of the total number of species of Tubifloræ. This tendency, it will be remembered, is not a marked feature in Archichlamydeæ, nor, indeed, among the Sympetalæ which we have considered so far.

A striking feature of the Tubifloræ is reflected in the fact that the large majority of the species comprised in this extensive group are herbaceous. We need only mention the familiar Convolvulaceæ, Boraginaceæ, Solanaceæ, Labiatæ and Scrophulariaceæ in illustration of this; and in the light of our observations in the preceding chapter (*supra*, p. 222), this feature possesses considerable importance as significant of advance.

Two fundamental characters stand out as almost unexceptionally constant throughout the Tubifloræ; first, the ovary is superior, and second, the carpels are two in number. It need scarcely be stated that the corolla is invariably sympetalous; and the stamens are epipetalous, sometimes at the base, but usually in the tube, throat, or mouth of the corolla.

The cohort Tubifloræ of Engler falls naturally into three main divisions. In the first, the connection between this cohort and the Contortæ is observable, the flowers being prevailingly regular or sub-regular, and the andrœcium isomerous with the corolla; this may be regarded as a transitional group. In the second and third divisions the flower is almost invariably zygomorphic; in one of these two the ovules regularly number two, rarely one, per carpel; in the other the number of ovules is prevailingly indefinite.

Bentham and Hooker ascribe cohortal rank to each of these three divisions, naming them respectively Polemoniales, Lamiales, and Personales. In Engler's system they are treated as sub-cohorts, or divisions of a single cohort, the Tubifloræ; further, the Acanthaceæ and Myoporaceæ are each assigned therank of separate divisions, making five in all.

It will be well to consider these three groups in order separately.

THE TRANSITIONAL GROUP.

This group, characterized by regularity of the flower and isomery of the andrœcium with the corolla, is represented by group A of Engler's system and the cohort Polemoniales of Bentham and Hooker; the typical characters of the natural orders comprising this cohort, together with the relations between the two systems, are displayed in the accompanying table. The essential difference between them is the inclusion by the older authors of the Solanaceæ in their transitional group; we shall have need to return to this important point later. For our immediate purpose we shall follow the older system in this regard.

The largest natural orders concerned, then, are Solanaceæ with 1,500 species; Boraginaceæ, with 1,200 species; and Convolvulaceæ, with 1,000 species. A brief consideration of the latter two leads to the conclusion that they both reflect high evolutionary advance, each upon a special line. The characters of the constituent species of both are remarkably constant throughout. The habit, in the first place, is characteristic in each case—the climbing, herbaceous or sub-herbaceous habit of the Convolvulaceæ, with their generally large, funnel-shaped flowers and alternate leaves,

ENGLER		BENTHAM AND HOOKER		APPROX. NUMBER OF SPECIES	ECONOMY TENDENCY					ADAPTATIONS TO INSECT VISITS
					SYMMETRY OF FLOWER	NUMBER OF STAMENS	PISTIL			
	NATURAL ORDER	COHORT	NATURAL ORDER				NUMBER OF CARPELS etc.	NUMBER OF LOCULI	NUMBER OF OVULES PER LOCULUS	
SUB-COHORT A	Convolvulaceae	POLEMONIALES	Convolvulaceae	1000	REGULAR	= C	$(\underline{2})$	2 or 1	2	Enlargement of individual flower
	Polemoniaceae		Polemoniaceae	200		= C	$(\underline{3})$, rarely 2 — 5	3	1 — ∞	,,
	Hydrophyllaceae		Hydrophyllaceae	170		= C	$(\underline{2})$	2 or 1	2 — ∞	Dense scorpioid inflorescences
	Boraginaceae		Boragineae	1200		= C	$(\underline{2})$	4	1	,,
In C	Nolanaceae		Nolaneae, a tribe of Convolvulaceae	50		= C	—	see text	1	Enlargement of individual flower
	Solanaceae		Solanaceae	1500	Usually regular, in some cases zygomorphic	= C or < C in † forms	(2)	2 or more	1 — ∞	Tendency to zygomorphy with oligomery of androecium

TABLE

SUMMARISING THE FLORAL CHARACTERS OF TUBIFLORÆ.

typically cordate at the base; and the scorpioid inflorescence of the Boraginaceæ, their surface hispid with coarse hairs. In the gynæcium these two orders display considerable advance, the ovules numbering constantly two per carpel. The Boraginaceæ shew still further specialization in the fruit character; the four one-seeded nutlets, whorled about a gynophore derived from the base of the gynobasic style, constitute a familiar feature. The flowers of this order, moreover, are highly specialized, in many cases, in relation to insect-visits, as witness the hairs or scales closing the corolla-mouth in several forms, the anther-cone in *Borago*, and so forth.

These two natural orders, then, must be regarded as relatively advanced, the Boraginaceæ considerably more so than the Convolvulaceæ. But there is very little indication in either of the fundamental tendency expressed in the large majority of the Tubifloræ, namely, zygomorphy of the flower coupled with oligomery of the andrœcium; such as there is will be referred to shortly. The same lack of such indication is observable in the other two natural orders of Engler's transitional group, Polemoniaceæ and Hydrophyllaceæ. These are relatively small orders, occurring chiefly in the new world; the first consists of about 200, the second of about 170 species. In both, the flower is regular and the stamens equal in number to the corolla-lobes. The members of both are advanced in so far that they have adopted the herbaceous habit in nearly all cases; but in regard to the tendency to ovule-reduction, referred to above, they are far less advanced than the Boraginaceæ, for the number of ovules is variable, although a tendency to reduction is traceable. The scorpioid inflorescence of Boraginaceæ is a common feature also in Hydrophyllaceæ, and may be regarded as a type of floral aggregation in relation to insect-visits comparable with the verticillasters and capitate inflorescences found so commonly in Labiatæ. The Hydrophyllaceæ are, moreover, exceptional in another direction; the ovary is typically unilocular.

The Polemoniaceæ are curious in regard to the carpel-number, which is invariably three; this constitutes the sole exception of any material extent to the constancy of the bicarpellary condition among Tubifloræ, and, indeed, among the so-called Bicarpellatæ as a whole (*supra*, p. 218). We shall refer to this point again when we approach the question of the origin and affinities of the group.

It is to the Solanaceæ that we must look for strong indications of that zygomorphy which is the essential character of the cohort under consideration. Quite 60% of the total number of species included in this order belong to the very natural genus *Solanum*, the flowers of which are of the type characteristic of what we have named the "Transitional Group"; they are regular, with isomerous andrœcium, and the bicarpellary ovary contains an indefinite number of ovules: this latter condition is virtually universal throughout the Solanaceæ. The flowers of *Solanum* shew specialization in the andrœcium, the anthers being connivent, often coherent and with an opening at the tip—much as in *Borago*.

For the remaining genera, most of the forms concerned are of the same "transitional" type; but a definite tendency to zygomorphy is observable in the greater or less development of the corolla-limb on one side (e.g., *Petunia*, *Nicotiana*), and also in the frequent inequality in length of the stamens even though these be isomerous with the corolla.

Similar hints at zygomorphy, rare but significant, are to be found among the the orders already considered—e.g., *Echium*, *Lycopsis*, *Macromeria*, in Boraginaceæ; *Bonplandia* in Polemoniaceæ. Another primitive form which zygomorphy may take consists in the lateral placing of the stamens relatively to the perianth, in flowers where the stamens are exserted. The flowers in such cases usually face laterally, or are pendulous, and the exserted portions of the filaments tend to hang downwards, more or less; but the terminal parts, bearing the anthers, are upturned. A good example of this is *Cobæa scandens* (Polemoniaceæ), a commonly cultivated greenhouse climber, but the phenomenon is by no means uncommon in flowers otherwise quite regular. Light doubtless has played a considerable part in the production of this condition, but the adaptation to the reception of insect-visitors is obvious. We shall have need to consider yet another type of Zygomorphy, the outcome of inequality in the calyx-lobes, when we deal with the Rubiaceæ.

Finally, in the tribe Salpiglossideæ, the number of fertile stamens is rarely so great as the number of corolla-segments; the andrœcium, in fact, is oligomerous in nearly 90 species (e.g., *Brunfelsia*, *Schwenkia*, *Anthocercis*), and the stamens are arranged didynamously in the manner characteristic of the Lamiales and Personales. Intermediate stages, in which one or more stamens are represented by sterile staminodes, occur; while the extreme case, in which the andrœcium consists of two fertile stamens only, is found in, *e.g.*, *Schizanthus*, a commonly cultivated plant with strongly zygomorphic flowers.

Taking the natural order Solanaceæ as it stands in our modernly accepted systems of classification, we find that only about 6% have obviously zygomorphic flowers. These, comprised in the tribe Salpiglossideæ, were originally included by Hooker in the Scrophulariaceæ,[1] and the constitution of Solanaceæ as a truly natural order is still a matter for debate. These zygymorphic forms display undoubted affinities with the sub-regular forms of Solanaceæ on the one hand, while on the other they pass almost insensibly into Scrophulariaceæ. The latter order, again, includes many sub-regular forms with isomerous andrœcium (*Verbascum*). It is apparent, then, that the line between the two orders in question is extremely difficult of description; as a result, they appear in the same sub-cohort in Engler's system. There is small doubt that research would reveal the necessity for no little rearrangement upon the border-line between the two orders; but our concern here is with the bulk of the species typical of each order. On one side we have the Solanaceæ, the large majority of which are more or less manifestly closely related *inter se*, and have regular or sub-regular flowers with isomerous andrœcium. On the other side we have the Scrophulariaceæ, the large majority of which have strongly zygomorphic flowers with oligomerous andrœcium. The claim of the small minority of Solanaceæ which have flowers with the two last-named characters to remain in this natural order must rest upon other critical features, and upon the strength of their relationship with the typical members of this order estimated in the light of those features; this, in any case, is beyond our present scope. Sufficient has been said, perhaps, to justify our inclusion of the Solanaceæ in the Transitional Group, in agreement with the system of Bentham and Hooker; and this order is especially important in the history of the group, in so far as it seems to lie, from the evolutionary aspect, very near to the direct line leading from an apocynal ancestry to the multiovulate zygomorphic Tubifloræ. The general question of the origin and affinities of this Transitional Group must now be approached forthwith.

In the first place, the bond between the Convolvulaceæ and the descendants of the apocynal stock appears to be remarkably close. Many Convolvulaceæ recall climbing, suffrutescent apocynaceous forms strikingly in habit and general appearance, while the essential floral characters are very similar. The former order is, it is true, notable for the constancy of the alternate leaf-arrangement, while most Apocynaceæ have opposite leaves; but the exceptions to the latter are by no means rare. The æstivation of the corolla in Convolvulaceæ is invariably contorted, as in the typical apocynal flower. Taken together, such considerations seem to point with no mean force to the conclusion that Convolvulaceæ are to be regarded as the relatively near descendants of the apocynal plexus—that is to say, of the progeny of the apocynal stock typified in various Contortæ. The fundamental advance which has been made upon the latter consists in the reduction of the ovules to a constant two per carpel. This reduction we have already recognized as a tendency in the Contortæ; the Convolvulaceæ represent the complete realization of this tendency; and with this has been coupled the tendency to the herbaceous habit,—a general feature of the Tubifloræ (*supra*).

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[1] See J. D. Hooker's Appendix to Le Maout & Decaisne, *A General System of Botany, Descriptive and Analytical*, Mrs. Hooker's translation (1873), p. 586.

Before the realization of this ovule-economy tendency had proceeded very far, however, the main line of tubifloral evolution—the line of zygomorphy—emerged (see diagram, p. 300). Very low down upon this line a side branch appeared, determined largely by the complete adoption of the herbaceous habit, the aggregation of the flowers into dense scorpioid inflorescences, and the unilocular condition of the ovary; this line has the Hydrophyllaceæ as its terminal point.

A short distance further along the zygomorphy line,—in other words, before the tendency to zygomorphy was realized to any great extent—a second side-branch appeared; this branch, terminated by the Solanaceæ, is to be regarded as a relatively short one, in view of the close connection between many typical Solanaceæ and the Scrophulariaceæ; the greatest divergence, indeed, is in the genus *Solanum* itself, with its very constant and somewhat specialized type of flower. This line of zygomorphy, notable for its early emergence from the ovule-reduction tendency line, will be traced ultimately to those multiovulate Tubifloræ in which the tendency to zygomorphy is realized—*i.e.* the Personales of Bentham and Hooker; these latter it will be convenient to refer to as *Multiovulatæ.* At some distance along the ovule-reduction line a branch emerged, leading to the Nolanaceæ, and determined by a tendency with which we shall deal at some length later (*infra*, p. 303)—the tendency to schizocarpy.

Near the terminal point of the ovule-reduction line, when its tendency was almost fully worked out, so to speak, a second line of zygomorphy arose, to be terminated ultimately by the zygomorphic

Tubifloræ which have only two ovules to each carpel (Lamiales); these we shall name *Diovulatæ.* A branch-line, leading to the Boraginaceæ, left this latter line early, in a way closely analogous to that of the Hydrophyllaceæ-branch of the "multiovulate-zygomorphy" line. In the inflorescence character, moreover, these

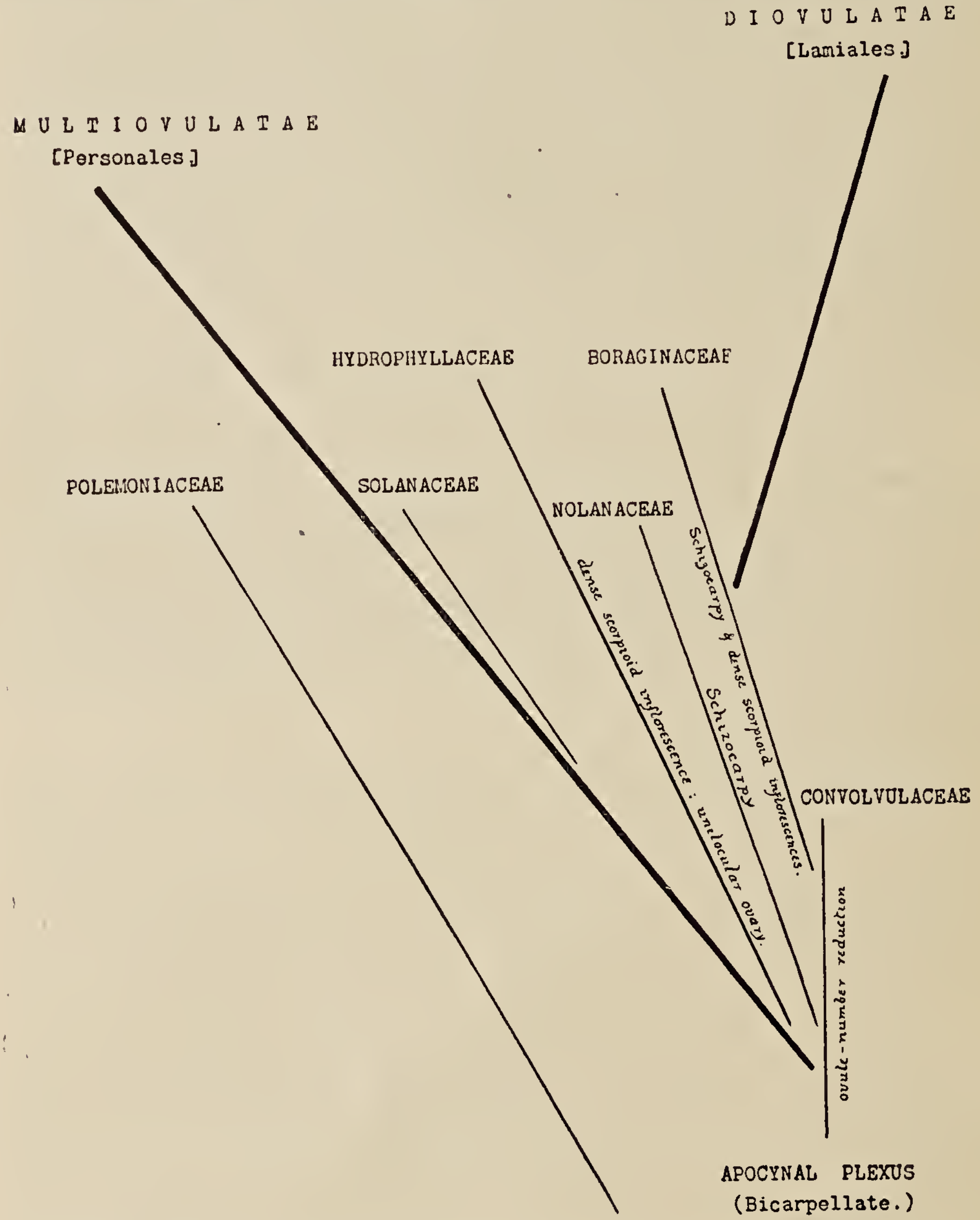

Diagram shewing possible affinities of the Transitional Group and its connection with the higher groups of Tubifloræ. The two thick lines represent the tendency to Zygomorphy.

two orders reflect one and the same tendency—a case, we must regard it, of parallel development; this is so indicated in the accompanying diagram, in which is summarized the foregoing sketch of the relationships of the orders concerned.

There remain for consideration the Polemoniaceæ. We have already referred to these as forming the only extensive exception to the bicarpellary condition of the ovary among the Contortæ and Tubifloræ taken as a whole—the ovary in Polemoniaceæ comprising, almost without exception, three carpels. For the rest, the corolla is invariably contorted in æstivation; the epipetalous stamens are equal in number to, and placed alternately with, the corolla-segments; the ovule-number is 1—∞ per carpel. The species are mostly herbaceous, rarely fruticose (*Cantua*).

It seems somewhat incongruous to include a very natural order, comprising 200 species characterized by a tricarpellary gynæcium, in a group of over 16,500 species every member of which has a bicarpellary gynæcium—*i.e.*, the so-called Bicarpellatæ. Some attempt has been made in these chapters to indicate the significance of the bicarpellary arrangement; but apart from any principles formulated here, the existence of some such significance is apparent from the mere fact that an ovary of two carpels is constant for an enormous number of species which are more or less closely related on other grounds.

The strongest claim for the inclusion of the Polemoniaceæ among the descendants of the apocynal stock would seem to be the isomerous and alternating epipetalous andrœcium; the primary economy principle has here reached its highest expression. But in the gynæcium, the working of the economy tendency has ceased at the stage which we have already noted as so common among the Archichlamydeæ (*supra*, p. 112); and in the essential characters the flower in Polemoniaceæ closely resembles many of the Ericales, such as Epacridaceæ, Diapensiaceæ, in so far the andrœcium is isomerous and alternating, and the gynæcium multilocular.

It would seem in all the circumstances that we must seek the ancestry of the Polemoniaceæ further back than in the apocynal stock, which is essentially bicarpellary. They may, indeed, represent a link between this stock and the Archichlamydeæ; and in this case they should find a place among Heteromeræ—as representative of a sympetalous group which adopted sympetaly before its primary economy tendencies were fully worked out. However, the discussion of the affinities of this order in any further detail is scarcely within our field; suffice it to say for the present that we shall regard the Polemoniaceæ as the descendants of a stock separate from the apocynal stock and not so advanced; this has been shewn on the diagram p. 300, where the similarity between this order and the Hydrophyllaceæ is indicated as the result of parallel development. It is conceivable that the Polemoniaceæ were derived from the geranial stock before carpel-economy had reached the bicarpellary stage, and before ovule-economy had proceeded even so far as in the Geraniales and Sapindales (see diagram below).

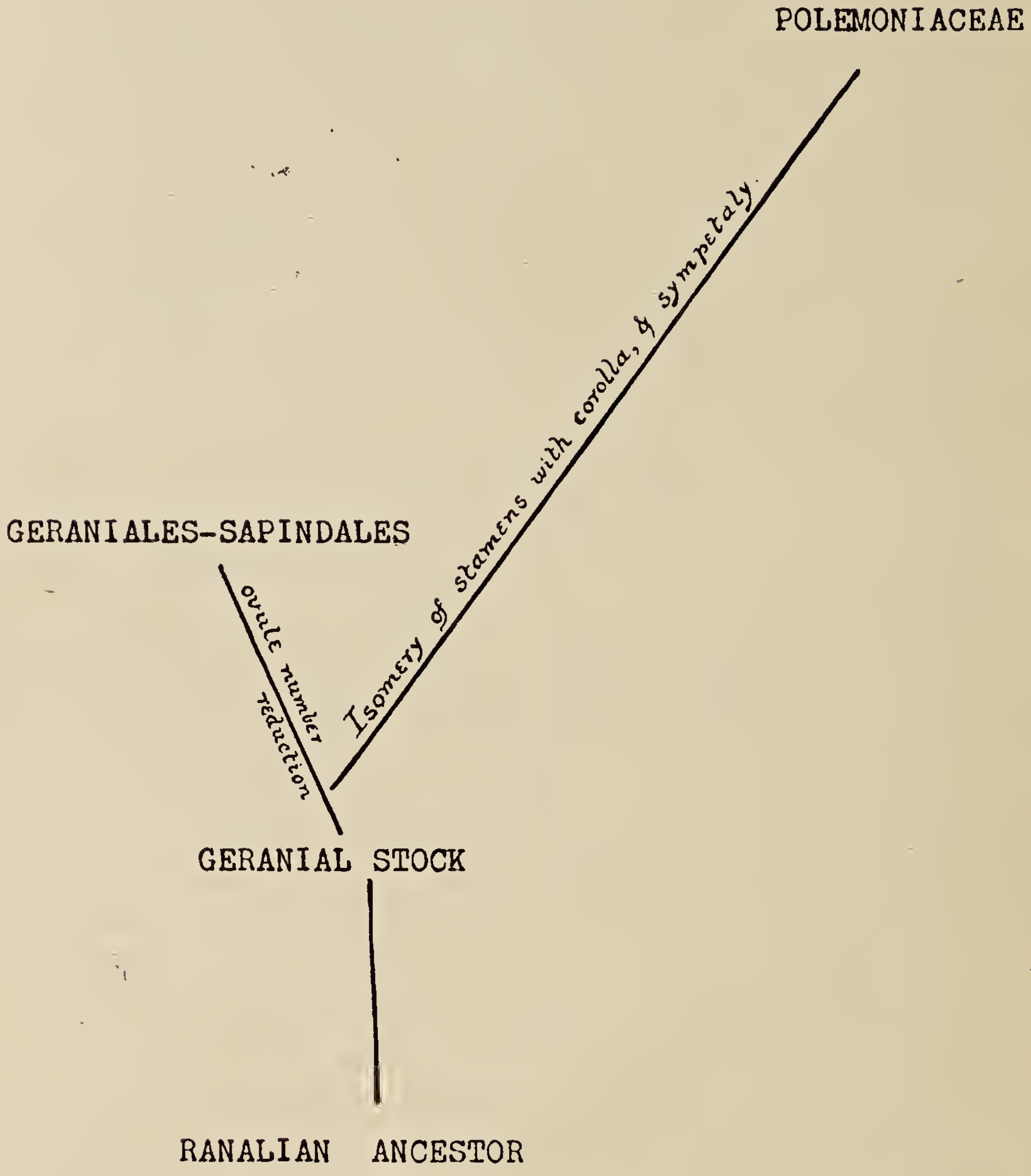

Diagram illustrating the origin suggested for the Polemoniaceæ.

In connection with the Transitional Group it is necessary to draw attention to a noticeable tendency in certain of its components, namely, to secondary or "spurious" septation of the ovary. The essence of this septation lies, presumably, in its initiation subsequently to the primordial development of the pistil; it results in the division of the ovary into a number of loculi exceeding the number of carpels. The problem in any particular case is, of course, intimately associated with development, and a wide and useful field of enquiry is open in this regard. For the number of loculi is by no means an infallible guide to the number of carpels, especially when this is an even number. In the case, say, of a three- or five-locular ovary it is tolerably sure that the carpel-number is at any rate greater than two. But a four-, six- or ten-locular ovary may be the product of two, three or five carpels. The Boraginaceæ offer a familiar example of this; in these the number of carpels is known to be two, typically, but the ovary is divided into four uniovulate compartments. The general biological significance of this phenomenon is not altogether obvious, but it may be suggested that, broadly speaking, it is connected with fruit and seed-dispersal, and its occurrence in any group may be regarded as at least an attempt in the direction of an efficient mechanism to that end.

The whole question is but one aspect of the broad general problem of the detailed structure of the ovary and its significance; and as this becomes a matter of increasing importance in the consideration of these higher groups, it will be well to take the present opportunity to discuss it at length. The closed ovary is the essence of the Angiosperm, and its primary object is ovule-protection. But this protection must not be afforded at the expense of efficient seed-dispersal; hence various devices have been evoked in the course of descent which are aimed to secure the latter end, the protective function at the same time being exercised as long as possible in the career of the seeds. The end in view is the conveyance of the seed to a spot suitable for its germination and for the subsequent development of the plant-body; that is to say, a greater or less distance has to be covered. The host of different types of fruit, with their varied mechanisms for dehiscence, dispersal, and so on, are all referable to this function of conveying the seed to a distance. In some cases evolutionary effort, if we may so express it, has been directed chiefly to the rapid dispersal of the individual seeds, which become independent of the fruit soon after maturity; such is the case with the comose seeds in the multiseminate follicles of Apocynaceæ and Asclepiadaceæ. But the general trend of descent in this regard seems to have been the combination of efficient dispersal with an extended period of protection, and this has been secured in the obviously most adequate way by the association of a single seed with a fruit-body. This in turn has been effected in various ways, all of which seem to fall under one or another of the following heads:—first, the apocarpous pistil, which, in the primitive form typified in Ranales, entails a considerable expenditure of material for each individual flower and so has been abandoned in the course of evolution in obedience to the principle of economy: second, the schizocarp, under which head the Boraginaceæ fall: and third, the unilocular fruit containing a single seed, the product of an uniovulate and unilocular ovary. In the light of this last consideration, the significance of economy in production of megasporangia, already noted in the present chapter, becomes increased, for the tendency to economy is seen to ally itself with the all-important function of seed-dispersal. The Compositæ afford the highest expression of this idea; the bicarpellary ovary here is unseptate, contains but a single ovule, and matures into a small one-seeded fruit dispersed usually by the agency of a pappus.

The schizocarp represents an alternative method of securing a fruit-body for each individual seed, and in so far as this latter condition characterizes an extensive section—about 30%—of Tubifloræ, we must regard it, in this group, as representing a general biological tendency comparable with zygomorphy in the relatively isolated flower; the Diovulatæ (Lamiales), we shall find, reflect the achievement of these two tendencies in combination.

In view of these considerations we may conveniently name this secondary septation of the ovary "the tendency to schizocarpy." We have already recognized it in a high degree of realization in Boraginaceæ, and the Solanaceæ represent an early stage in its progress; we shall meet with it again as a critical character of the Diovulatæ. The South American Nolanaceæ, comprising some 30 species, all herbaceous, afford a curious illustration of one way in which this tendency has achieved its aim. In these plants the structure of the ovary is similar to that of Boraginaceæ, but septation in all directions has resulted in the production of an indefinite number of uniovulate chambers, more or less free, some superposed above others, and surrounding the base of a gynobasic style. Originally classed by de Jussieu with Boraginaceæ in view of the last-named character, the Nolanaceæ were included in Solanaceæ by Duval and Baillon, and in Convolvulaceæ by Bentham and Hooker. The character of the pistil, however, seems to justify their rank as a separate natural order, in accordance with Engler's system where they are associated with Solanaceæ; but their regular flower and isostemonous andrœcium urge their inclusion in the Transitional Group, and their affinities appear to be rather with Boraginaceæ, with a proximate convolvulaceous ancestry.

The question of *secondary* septation of the ovary must be distinguished carefully from that of its *primary* septation; the latter is one of extreme difficulty, and it is desirable in these papers to avoid if possible the necessity for more than the mere statement of it. In so far as the angiospermous ovary is to be regarded as composed of sporophylls or carpellary leaves, whether by the folding of one leaf, of by the fusion of more than one, it will be reasonably conceived that the most primitive ovary would be unseptate—*e.g.*, the typical apocarpous carpel of Ranales. Septation is the result of more than one cause; it may be the consequence of inturning of the carpellary leaf-margins; of projecting placentæ; or of the organization of membranes to serve for the special purpose of chambering the ovary, as is the case with the secondary septa to which we have already made reference; but it is doubtful how far, if at all, this last condition obtains in the primary septation of the ovary. A septate ovary, again, may be the phylogenetic product of the union of apocarpous carpels. The problem in each case is one of floral development from the primordia to maturity, and any conclusions unbased upon actual research in this direction may be only worse than useless.

In certain cases, however, the progression to what we may name *secondary* unilocularity of the ovary may be traced in the observation of a series of allied forms as the outcome of degradation of septa; and it is urged that the higher groups characterized by a unilocular ovary may not impossibly be descended from stocks with septate ovaries in this way, the loss of the septa being sometimes correlated with reduction in the number of ovules. A case in point (except in the last-named particular) is that of the Primulales, with their "free-central" placentation, descendants of the caryophylline stock, in which the basal placenta which projects into the single chamber of the ovary is derived admittedly from an aggregate of degraded septa.

We shall have need to resort to some such tentative considerations as have been briefly sketched above in the study of the higher groups which we are now about to approach. In the absence of experimental evidence based on observation of the ontogeny of floral forms, we must take broad general considerations of biology as our guide in these questions of phylogeny and descent; but we cannot insist too strongly on the fact that our conclusions throughout amount to no more than mere suggestions as to the possible course of descent along a few main lines, together with some indication, perhaps, of the lines along which research might usefully be directed.

We now leave the Transitional Group and proceed to deal, in the next chapter, with the progeny of the stock which it represents.

(*to be continued*).

THE INTERNATIONAL PHYTOGEOGRAPHICAL EXCURSION IN THE BRITISH ISLES.

III.—The Floristic Results.

The first International Phytogeographical Excursion through the British Isles in August last, which had been so admirably planned by Mr. A. G. Tansley, with the help of his colleagues of the British Vegetation Committee, who acted as genial and accomplished guides, and often dispensed a gracious hospitality, proved a great success, since the visitors included not only distinguished ecological authorities like Professors Drude, Schroeter, Cowles and Clements, and expert botanical photographers like Professor Massart; but also such critical field botanists as Professor Lindman and Dr. Ostenfeld, and erudite botanical systematists like Professor Graebner. Therefore the writer, who had the privilege of accompanying the party throughout the extensive and wisely selected route through the British Islands, has to express his gratitude for the unique opportunity afforded of getting in touch with the views of his Continental *confrères*, and to offer his thanks to all the members of the party, and to the various leaders for their unvarying kindness. May he take this opportunity of saying that he feels, as a floristic botanist, that in future he must not be content with merely looking at or studying the individual, but must also investigate its neighbours and environment? So also he ventures to suggest that phytogeographers must not be satisfied with knowing "big" species only, but also be able to discriminate the more critical forms, since these are often special adaptations, and may prove the key to more than one vexed problem.

The following notes on some of the rarer, or more specially interesting plants observed on the journey may not, it is trusted, be considered out of place in these pages. It will be observed that through the acumen of Dr. Ostenfeld, a new waterlily and a Lady's Mantle have been added to our flora, that Professor Massart pointed out a new "variety" of *Sagina nodosa* and that Dr. Graebner urged that *Juncus ranarius* has claims to specific rank. Professor Graebner also showed the members a variety *Erikæ* of *Calluna vulgaris*, which Professor Ascherson had named after Professor Graebner's wife, Frau Erika Graebner, while Dr.

Lindman directed attention to a hitherto undescribed form of *Polygonium aviculare*, and Dr. Moss demonstrated the characters of several species of *Salicornia* and *Quercus*, which are described in his excellent papers on those genera.

It may be added that the writer has purposely left almost unnoticed the Brambles and Roses, and has left unmentioned not only many of the planted trees observed, but numerous other forms which still require elucidation.

The names of plants presumably new in name to Britain are printed in heavy type. A dagger (†) before a locality or county means that it is an addition to the records in Watson's *Topographical Botany* and Mr. Arthur Bennett's *Supplement* thereto. An asterisk (*) before a name means that the plant is alien to the British Flora, before a locality that the plant is presumably alien to that locality. The sign × means a hybrid. The numbers after a locality refer to comital numbers of *Top. Bot.* and *Irish Top. Bot.* The sequence and nomenclature is that of the writer's *List of British Plants*, which by the kindness of the Delegates of the Clarendon Press was supplied to all the foreign members of the party.

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4. *Thalictrum minus* L., in one of its numerous forms was observed on an island in the Lower Lake, Killarney 2.

T. collinum Wallr. is recorded for Killarney in the *Cybele Hibernica.*

20. *Ranunculous acris* L. On Ben Lawers 88, the plant which Herr Freyn of Prag names for the writer *R. Nathorstii* Berl. was observed at high elevations. The variety *Boræanus* (Jord.) occurred at Roundstone, Galway 16.

22. *R. bulbosus* L. occurred in flower as a form with deeply cut leaves (perhaps *brachiatus* Schleich.) on the limestone rocks, near Ballyvaghan, Co. Clare 9.

24. *R. Flammula* L. as the sub-species or species 26. *R. Scoticus* Marshall was noticed in loughs about Craigga More, but it may be that this form is not quite identical with the Scottish specimens. Dr. Glück is going to test its permanence of in cultivation.

48. *Caltha palustris* L.: a form of this with smaller but contiguous sepals occurred on the margins of one or two of the Norfolk Broads, flowering in August.

49. *C. radicans* Forster, near Butterston Loch,† Perth 7 E. 89.

77 bis. **Castalia candida** (Presl.) Schinz & Thellung (*Nymphaea candida* Presl. Delic. Prag. 224), was pointed out by Dr. Ostenfeld in a loch in the Dunkeld policies, †East Perth 89. In this locality it was in company with introduced species, and might possibly have been introduced with them. But its occurrence in undoubtedly

native localities in Ireland makes it probably of widespread occurrence in Western and Northern Britain. The plant is closely allied to C. *alba* Wood, the common white waterlily, and in some parts of Germany where they are frequent, the two forms are sometimes with difficulty separated. The distinguishing characters are the absence of stamens from the upper part of the ovary, leaving the neck bare; the pollen grains are smooth (not tuberculate as in *alba*), and somewhat larger. The lowest pair of leaf-veins are curved, and if produced would cross, inclosing an oval area.

The plant occurs in Finland, Sweden, Poland, Germany, Switzerland, Austria, Bohemia, Hungary, Tyrol, Siberia, Kashmir, etc., and, attention having been directed to it, will probably be found to the more frequent form in Scotland.

At †Craigga More 16, Co. Galway, Dr. Ostenfeld found it in a small Lough west of the road, and independently the writer found another on the east side, and also at †Roundstone, Co. Galway 16.

126. *Radicula palustris* × *sylvestris*. A plant which possibly has the above parentage, but in facies is very much nearer *sylvestris*, was noticed many years ago by the writer at Perth, on the west-side of the Tay 89. On this visit it was also noticed on the east-side of the river in some quantity. The plant is sterile and the petals scarcely open.

128. **Barbarea verna* Aschers., Perth 89.

133. *Arabis hirsuta* Scop., Silverdale, Lancashire 69.

161. *Draba incana* L. Monsal Dale, Derby 57, Ben Lawers 88, frequent. [A sure index to calcareous soils, occurring in shell-sand at the sea level in East Ross 106].

185. **Sisymbrium orientale* L. †Clifden, on the railway (Schroeter) and on the shores of Galway Bay.

217. **Brassica alba* Koch., on the shores of Galway Bay.

207. **Diplotaxis muralis* DC. †Clifden, on the railway, Galway 16, and also at Queenstown Junction; a distinct follower of the iron-road and thus gaining extension of its area year by year. The bare ballast, with few competitors, is its favourite home.

232. *Bursa pastoris* [=*Capsella Bursa-pastoris*] Weber var. *cuneata* Druce. Millers Dale, Derby 57. Honley, Yorks. 63. Southport, Lancashire 59. Penrith, Cumberland 70.

239. **Lepidium perfoliatum* L. Alien, Galway Bay.

293. *Viola sylvestris* Kit. On the limestone rock, near Ballyvaghan,† Co. Clare 9. A specimen of the above species was found in flower in this locality on August 23rd.

294. *Viola Riviniana* Reichb. A luxuriant cleistogamous form, forma *villosa* (N.W.M.) of this plant (teste E. S. Gregory) was noticed at Killarney.

Var *diversa* E. S. Gregory, Rep. Bot. Exch. Club, 496, 1910, at †Ballyvaghan, Co. Clare.

296. *V. canina* L. On Ben Lawers (Mid-Perth 88), at an altitude of 2,500 to 3,000 feet, this plant occurred as a large cleistogamous form, which suggested to Professor Graebner, but since his return to Berlin he refers it to *canina*, a conclusion also arrived at by Mrs. Gregory and the writer.

301 bis. *Viola epipsila* Ledebour. [This plant, which was recorded in the *Report of the Exchange Club* for 1910, p. 497, as

having been noticed in a sheet of *Viola palustris* from Hamilton Tor, S. Devon, collected by Mr. W. F. Miller of Winscombe. In June, 1911, the writer was fortunate enough to find the plant in some plenty in several places near Moreton Hampstead and Widdycombe. Although essentially lowland, and a nature of alder swamps and shady places, it also occurred in some bare elevated places on Hamilton Tor. The appearance of the plant at once reminded the writer of a plant he had seen at Burghfield, Berks, about 1890, and on his return he visited that locality where he found *V. epipsila* in some quantity and in a similar situation. But similar localities in Bucks only yielded *V. palustris.*] At Killarney, near the upper lake, the writer again met with this form, thus adding a new plant to †Ireland, Kerry 2. The hairy petioles and the hairy nerves on the under leaf surface, together with a slightly more pointed end to the leaf are distinguishing features, but the plant is very closely allied to *V. palustris*, from which, however, Becker in his recent monograph keeps it distinct. In Europe it appears chiefly as a northern plant, so that its occurrence in Devon and Kerry was somewhat unexpected, especially as the apparently suitable home among sphagnum and alder, at Dunkeld only afforded *V. palustris.* Mrs. Gregory assents to the name.

333 bis. **Saponaria orientalis* L. An Eastern alien. Occurred by †Galway Bay 16 with other casuals.

334 b. *Silene amoena* L. (=*S. maritima*) var *parvifolia* (Druce). This small-leaved Sea Campion which the writer found on the shingle of Looe Bar, Cornwall, was also found this year (F. Hamilton Davey). Its correct name, however, is *S. maritima* With. var. *parvifolia* Druce, as given in the *List of British Plants*, since *S. amoena* L. Sp. Pl. 1753, from Siberia, is almost certainly a distinct species. Another form of *S. maritima*, which is worth further study, occurred close to Ross Castle, Killarney. The type occurred in plenty on the shingle beach at Blakeney, Norfolk, W. 28.

368. *Cerastium alpinum* × *vulgatum* = × *C. Symei* Druce in Bot. Exch. Club Report 498, 1910. Ben Lawers 88 with both parents, agreed to by Dr. Ostenfeld.

370. *C. vulgatum* L. var. *longirostre* (Wichura). Ben Lawers 88. var. *hirsuta* Fries. †Foulshaw, N. Lancashire 69.

374. *C. tetrandrum* Curtis. Blakeney, Norfolk, W. 28. Roundstone, Galway 16.

382. *Stellaria Dilleniana* Moench. Near Sutton Broad in two stations. Growing with *S. Dilleniana* var. *palustris* (Retz.) (=*S. glauca*), and flowering at the same time; thus supporting the writer's contention (*Bot. Exch. Club Report*, 546, 1910), that the two plants are not specifically distinct. Professors Graebner and Lindman both know the plant well, and are of the same opinion. In some parts of Sweden, this green plant is much commoner than the glaucous variety.

383. *Stellaria graminea* L. var. *latifolia* (Godron) Rouy and Fouc. iii., 234, 1896. Under this would come robust, large-leaved plants which grow near Dunkeld, E. Perth 88, and near Perranwell, Cornwall 1.

399. *Sagina nodosa* Fenzl. var. *glandulosa* (Besser Prim. Fl. Galilc, ii, 359, 1809) = *S. nodosa* var. *pubescens*, Mert. & Koch, Deutsch Fl. iii, 362, 1831. †Galway 16, sometimes as a very luxuriant tufted plant.

†Var. *simplex* Graebn. N. G. Danzic, N. F. 1. 362, 1896, with the type (*e. glandulosa*) on the Southport dunes 59.

Var. **moniliformis** (Meyer Chlor. Hann., p. 206, 1836, under *Alsine nodosa*) Lange. Meyer's (l.c.) brief description is "Kurzblätterige, Blätter knorrige Miene." Professor Graebner agreed to this determination, and Professor Massart pointed out the latter plant to the party growing in "slacks" on the Southport dunes, where it was abundant. [Mr. W. G. Travis shows (*Journ. Bot.* 270, 1911), that this variety affords an interesting instance of vegetative reproduction.]

407. *Sagina maritima* Don. On the shingle at Blakeney, Norfolk, W.

403 bis. **Sagina glabra** Fenzl. Verbr. Alsin. t. ad., p. 57, 1833. *S. repens* Burnat in Gremli Fl. Schweiz, ed. 3, 100. *Spergula glabra* Willd., Sp. Pl. ii, 821, 1799. *S. saginoides* All. Fl. Ped. t. 64, 1785. *S. repens* Zumagl. Fl. Ped. ii, 286, 1864. *Spergella glabra* Reichb. Ic. Fl. Germ. et Helv. t.ccii. f. 4964. This plant was noticed by the writer on the lower slopes of Ben Lawers 88, by the large burn which descends from the Gentian rocks, and was, at first, a complete puzzle. It suggested a large-flowered *S. saginoides*, or a creeping form of *S. subulata*, or perhaps a pentamerous petaloid *S. procumbens*, but as fresh plants were found, one after another of these suggestions was dismissed as untenable The plants were in considerable quantity and in free flower on this hot sunny day, at a much later date (August 17th) than the writer had ever been on the hill. Dr. Ostenfeld became inclined to refer them to a hybrid of *procumbens* and *saginoides*, but the plants were fertile and commoner than either of the assumed parents. Professor Graebner agreed with the writer in assigning them to a distinct species. The plants occurred on an altitudinal range of from 1,200 to 3,500 feet. Subsequent comparison leads the writer to refer them to the above species, which occur in "prairies sablonneuse" in the Alps of Switzerland, France, Italy and the Tyrol. The chief difference appears to be that in the Scottish plant the capsule is somewhat smaller. From *S. saginoides* it may be known by its large flowers, though doubtless in herbaria it will be often found to represent that species. From *S. subulata* its more creeping habit and more woody root stock will distinguish it. Owing to the difference in the capsule it may be worth while distinguishing the Scottish form from the Continental species as var. *scotica.*

402. *S. nivalis* Fries. In some plenty this year on Ben Lawers and with it plants which Dr. Ostenfeld considered to be *nivalis* × *saginoides.*

403. *S. saginoides* Dalla Torre. On Ben Lawers up to 3,800 feet, but over flower. (*S. glabra* was in full blossom).

411. *Spergularia rupestris* Lebel. Plentiful at the Lizard 1.

421. *Montia fontana* L. (M. lamprosperma Cham.) Chewbrook Clough† 63, Ben Lawers 88, Killarney, †Kerry 2.

421 bis. *M. verna* Necker. †Near Dunkeld 89, practically new to Scotland, but specimens from Fife 85 are in *Herb. Edin.* Perranwell, Cornwall 1.

424. *Elatine hexandra* DC. Looe Pool 1.

479 bis .**Geranium Endressi* Gay in Ann. Sci. Nat. Sér. i. t. xxvi, 228, 1832. This ornamental alien species from the West of

Europe occurred in the woods of Woodsome Hall, Yorkshire 63, where it was doubtless introduced.

488. *G. Robertianum* L. var. *purpureum* Forster. †Galway Bay 16.

†Var **Villarsianum** Jord. Ballyvaghan, Co. Clare 9.

497. *Erodium cicutarium* L'Hérit. var. *glandulosum* Bosch. on the sand dunes at Southport 59: Roundstone, Galway 16.

500. **Tropæolum peregrinum* L. Alien †Galway Bay 16.

513. *†*Impatiens glandulifera* Royle and its var. *pallida*. Mallow, Ireland 5.

519. *Rhamnus catharticus* L. †var. **Schroeteri.** This plant which was conspicuously different from the type by its more yellowish-green foliage and by the leaves being covered with a mealy pubescence was first noticed by Professor Schroeter by the roadside in Silverdale 69. It was in good fruit.

528. **Lupinus nootkatensis* Donn. On the shingly margins of the Tay near Aberfeldy 88.

538. *Ulex Gallii* Planchon was in good flower by the roadside above Honley, York 63, at the foot of Crossfell near Kirkland, and was in magnificent show at Roundstone and on the hillsides by Galway Bay (with var. *humilis* Planch.) 16 and also at the Lizard 1, etc.

539. *Ulex minor* Roth (=*U. nanus* Forster) characteristic on the heath on Bow Hill, north-west of Chichester, and on the New Forest heaths.

597. **Melilotus indica* All. Alien on the shores of Galway Bay †16.

599. *Trifolium pratense* L. var. *americanum* Harz. †Near Dunkeld 89.

683. **Vicia varia* Host. This beautiful European vetch also occurred as an alien at †Galway Bay 16.

746. *Spiræa Ulmaria* L. var. *denudata* Boenn. Woodbastwick, etc., Norfolk 27. This variety keeps true not only in cultivation but from seed. The result of Professor Yapp's experiments are awaited with interest.

879. *Rubus saxatilis* L. Monsal Dale 57.

880. *R. Chamæmorus* L. A most striking feature in the vegetation of the upper part of Blackchew Head Moors 63, but mostly barren.

881. *Dryas octopetala* L. In the greatest abundance near Ballyvaghan 9, and still in flower August 23rd.

888. *Potentilla fruticosa* L. The abundance of this local species proved a great joy to the foreign members when they saw it in one of the turloughs near Ballyvaghan 9, and repaid them for their early rising.

890. *Potentilla Anserina* L. On the bare sand of Roundstone Bay 16 this plant appeared in an interesting modification, the runners spreading over a circuit of 4 feet. The plant was the var. *discolor* Wallr.: upper surface of leaves green and glabrous, the under surface densely covered with silvery pubescence.

900. *P. verna* L. Silverdale 69.

902. *P. procumbens* Sibth. Greenfield 63, Silverdale 69, Lizard and Truro 1, Roundstone, Galway 16, Killarney 2.

902. *P. procumbens* × *reptans*=*P. mixta* Nolte. To this hybrid

may probably be referred a pretty plant which grew on the bank of the road near Truro, where Mr. F. Hamilton Davey found it in some plenty.

903. *P. erecta* × *procumbens* Sibth. A plant with distinctly petiolate leaves which is probably this hybrid occurred on the †Lizard Downs 1.

909. *Alchemilla vulgaris* L. var. **acutidens** (Buser) Briquet in Burn. F. Alp. Marit iii, 149, 1899. =*Alchimilla acutidens* (Buser) Bull. Herb. Boiss. ii, 104, 1894. Lindberg Die nord Alchimella vulgaris-Formen, p. 111, t. 16, 1909). Pointed out by Dr. Ostenfeld on a rock in the Carie Burn running from the west side of Ben Lawers at about 1,200 feet, and in many places up to 3,500 feet on Ben Lawers, and on rocks above Lochan 'a Chat 88.

It is found in Iceland, Faroes (Ostenfeld), Norway, Sweden, Finland and Russia, and thus was likely to be found in Scotland. The writer is at present unable to find any *strong* distinguishing features by which to separate it from the var. *glabra* DC. (=*A. alpestris* Schmidt).

909. *Alchemilla vulgaris* L. var. *minor* Huds. (=*A. filicaulis* Buser *vestita*). Greenfield, Yorks 63, Silverdale 69, Ballyvaghan, Co. Clare 9.

914. *Agrimonia odorata* Miller. Roundstone, Galway, 16.

945. × *Rosa involuta* Sm. In one of its protean forms this hybrid was seen in Monsal Dale 57, for which place *R. Doniana* and *R. Robertsoni* are recorded in *Flora Derby*, 135, 1903.

957. *Pyrus Aucuparia* Ehrh. var. (or forma) **flava.** The Mountain Ash with orange-yellow fruits was shewn to us by Dr. Ostenfeld at Roundstone, Galway 16, and it also occurred at Killarney 2.

959. *P. intermedia* Ehrh. As a planted tree at *Greenfield, Yorks 63, and passed as this species by Professor Graebner.

961. *P. Aria* Ehrh. var. *rupicola* Syme on the limestone rock, at Silverdale 69.

966. *Cratægus Oxyacantha* L. (=*C. monogyna* Jacq.) var. *cuneata* Druce. †Clifden, Co. Galway 16.

972. **Cotoneaster microphylla* Wallich. Was seen naturalised in several places and *C. Simonsii* Baker *near Clifden, Galway 16.

978. *Saxifraga rosacea* Moench (*decipiens* Ehrh.) Ben Lawers, attested by Professor Graebner.

996. *Chrysosplenium alternifolium* L. At 3,000 feet and upwards on Ben Lawers.

999. **Escallonia macrantha* Wedd. Naturalised, †near Clifden, Galway 16.

1000. *Parnassia palustris* L., as a dwarf plant with very large flowers and fruit at Southport 59, in the damp "slacks" of the sand dunes.

1010. *Sedum Telephium* L. var. *Fabaria* Koch (? *purpureum* L.) in Silverdale 69, and by the Tay, Perth 89. There appears to be some doubt in the minds of our foreign *confrères* as to whether we have the true *S. Telephium* L. in Britain. All the plants seen were referred by them to the above form.

1015. *S. acre* L. Professor Schroeter and Professor Graebner considered that the *S. acre* as seen by them in Norfolk 28, Miller's Dale 57, Southport 59, Westmoreland 69, and Cumberland 70 was not the German or Swiss plant. Professor Graebner is going to test it in cultivation.

1033. *Myriophyllum alterniflorum* DC. Common in Butterston Loch, etc., Dunkeld, E. Perth 89. Also in streams and loughs near Roundstone 16, and Killarney 2: in these localities the plant was often very dwarfed and the leaves very short.

1040. *Callitriche autumnalis* L. Butterston Loch, E. Perth 89.

1042. *Peplis Portula* L. At Killarney 2, a form of this plant was found in which the calyx-teeth were long—thus approaching the var. *longidentata*, J. Gay and the writer proposes to distinguish this plant as var. **dentata** to distinguish it from the common plant of Eastern Britain in which the calyx teeth are short or obsolete. The Atlantic and Mediterranean plant is usually var. *longidentata.*

1047. *Epilobium hirsutum* L. with wholly female flowers in Silverdale 69.

1051. *E. obscurum* × *parviflorum* †Clifden, Co. Galway 16.

1052. **E. roseum* Schreber. As a garden weed in Lancaster 60, Greenfield 63 and by the Tay at Perth †89.

1056. *E. alpinum* L. Huds. Crossfell at about 2,600 feet 70.

1064. **Œnothera Lamarkiana* Ser. in several mutations near Southport 59.

1071. **Fuchsia Riccartoni* Hort. In magnificent flower and quite naturalised near Clifden and Roundstone, Galway. No specimens in fruit were found. Does it produce seed?

1073. *Circæa intermedia* Ehrh. By the Tay at Perth 89, also by Loch Tay 88, perhaps rather a distinct species than a variety, and possibly originally a hybrid of the two other species which has become " fixed."

1077. **Mesembryanthemum* sp. Abundantly naturalised near Penrose, Cornwall. The specific identity is apparently somewhat doubtful. In Davey's excellent *Flora of Cornwall* it is referred to as *M. aequilaterale*, Haworth, but the name *M. acinaciforme* L. was suggested by some of the foreign visitors.

1100. *Cicuta virosa* L. In great plenty and in beautiful colouring in the Norfolk Broads 27.

1118. *Chærophyllum aureum* L. was found in great quantity (in the original station, see Bot. Exch. Club) by the Teith at Callander 87 where the consensus of opinion was in favour of its being native there. It was " one of Don's reputed discoveries "!

1133. *Œnanthe fluviatilis* Colem. was seen in abundance near Cambridge, etc. This plant, long considered to be endemic, has been found plentifully in Germany and Luxembourg by Professor Glück.

1153. *Heracleum Sphondylium* L. At 3,000 feet on Ben Lawers 88, as a glabrous plant=var. *glabrum* Koch.

1172. *Hedera Helix* L. The plant of Silverdale had much narrower leaves on the flowering shoots than the midland plants, but not quite so extreme as in the Skye Ivy.

1175. **Cornus stolonifera* Michx. By the Tay 89.

1196. *Galium sylvestre* Poll. Monsal Dale 57, Ben Lawers 88.

1198. *Galium Witheringii* Sm. Sutton Broad †27. Perhaps a distinct species.

1214. *Sherardia arvensis* L. var. *maritima* Griseb.=(*Asperula Sherardi* var. *maritima*). Roundstone, Galway †16. A form with the calyx teeth nearly obsolete.

1240. *Eupatorium cannabinum* L. with undivided leaves at the Lizard 1, but probably not the *indivisa* DC.

1243. *Solidago Virgaurea* L. This variable plant was observed as var. *cambrica* (Huds.) on Ben Lawers, as a narrow-leaved plant (var. *angustifolia* Koch) at Killarney, and as a very stout dwarfed form with sub-capitate inflorescence, with leaves varying considerably in width and the outer florets scarcely so large as in *cambrica* on the Lizard Downs. Comparative culture of these forms could not fail to give interesting results.

1258. *Aster Tripolium* L. with discoid capitula in many places, Hayling Island, S. Hants 11, North Bull, Co. Dublin 21.

1283. *Inula crithmoides* L. Hayling Island near Havant 11, fringing the salt marsh and in good flower.

1291. **Ambrosia artemisifolia* L. An alien doubtless introduced with chicken food at Havant, †S. Hants 11.

1297. **Rudbeckia laciniata* L. in plenty by the Tay at Perth 88, 89, where it has long been naturalised.

1298. *Achillea Ptarmica* L. in upland pastures near Greenfield, S.W. Yorks 63, as a smaller and more compact plant than usual.

1338. *Anthemis nobilis* L. Rather common about Clifden and Roundstone, Galway 16.

1360. *Matricaria inodora* L. var. *maritima* (L.) Culture in this case is much needed, as there are two or three maritime forms, which require investigation. Roundstone, Galway 16.

1362. **M. suaveolens* Buck. The rapid advance of this American species through Britain is most remarkable. It follows the roads and may owe its origin in many cases (as *Juncus tenuis* probably does) to American fodder or corn. It was noticed near Sutton Broad, †Norfolk, E. 27, Derby 57, Yorks, S.W. 63, Lancashire 59, Cumberland 70,† Westmoreland 69, and in Co. Galway, Dublin, and †Cork.

1376. *Artemisia maritima* L. Rather plentiful near Blakeney, and under two modifications, one much less hoary than the other and forming distinct patches on the salt marsh. It was still too early in the year (August 6th) to be certain whether these were the type and the var. *gallica* (Willd.) respectively. The latter has erect capitula. It was found in flower at Hayling Island on September 3rd.

1394. *Senecio Jacobæa* L. var. *discoideus* L. Plentiful near the coast at Roundstone, although plants of the well marked rayed form were in the vicinity. [The rayless form of the Ragwort was noticed by Sherard near Drogheda prior to 1724 when it is recorded by Dillenius in the *Synopsis*.]

1401. *Senecio vulgaris* L. forma *crepiformis*. Blakeney, Norfolk, W. 28, on the bare shingle. A curious form in which the capitula instead of being cylindric or nearly so as is usually the case, were extremely broad at the base like a *Crepis*. [An exactly similar form occurs at Pyrford, Surrey 17 where its curious looking capitula attracted the attention of Lady Davy who took the writer to see it. This character may be caused by a gall.]

1410. **Calendula officinalis* L. as an alien at Galway Bay †16.

1420. *Arctium nemorosum* Lejeune. Frequently seen on the excursion, as at Monsal Dale, Derby 57, Silverdale †69, near Kirkland †70, near Dunkeld †89, Roundstone, Clifden, Co. Galway †16.

1434. *Cirsium palustre* Scop. var. **ferox** mihi. Near Silverdale and near Carnforth 69, on the slopes of Crossfell 800-1400 feet, often white flowered, Cumberland 70, on the roadside near Dunkeld, E. Perth 89, and Lawers, near Perth 88.

A most strongly spinous plant with more condensed inflorescence than the type. The spines are pale coloured and the foliage of a paler green. The continental botanists agreed that it was quite a distinct form from typical *C. palustre* and suggested that it should be separated as a variety from the type. It may perhaps prove to be the Spanish plant var. *spinosissimum* Willkomm.

1638 var. K. *Hieracium umbellatum* L. var. **dunale** G. Meyer. Southport sand dunes 59 in great quantity and although varying in stature well marked by the abrupt transition from long to shorter leaves.

1644. *Leontodon nudicaule* Banks (*L. hirtum* L.) var. *lasiolena* Druce, Southport 59. At the Lizard the common plant was the var. *leiolena* Druce.

1646. *Taraxacum spectabile* Dahlst. var. *maculigerum* Dahlst., near Woodsome, York †63.

1656. *Sonchus arvensis* L. var. *angustifolius* Meyer, Blakeney 28.

1657 *S. oleraceus* L. var. *runcinatus* Coss. & Germ. Galway †16.

1666. *Jasione montana* L. var. *litoralis* Fr. Clifden, Galway 16.

1687. *Oxycoccus quadripetala* Gilibert (=*Vaccinium Oxycoccus*). In some quantity on Foulshaw Moss 69, passed by Professor Lindman as the typical plant; a smaller plant with narrower leaves of a slightly different outline which grew sparingly in Crowden Clough, Cheshire 58, Professor Lindman thought might possibly prove to be *Oxycoccus microcarpus* Turczaninov. At Foulshaw Moss 69, the Cranberry was associated with *Andromeda Polifolia* L.

1693. *Calluna vulgaris* Hull var. **Erikae** Ascherson and Graebner.

On the moors near Wessenden Head, Yorks, pointed out by Professor Graebner: near Honley, Yorks: also on Ben Lawers 88, but scarce at 2,800 feet; at Dunkeld, E. Perth 89: also on Urrisbeg near Roundstone, Co. Galway 16: at Killarney, Co. Kerry 2: and on the Lizard moors above Kynance, Cornwall 1.

A handsome white-flowered form is cultivated in the Edinburgh Botanic Garden.

This rooting prostrate plant with descending flowering branches, Professor Graebner says retains its character in cultivation at the Berlin Garden.

1694. *Erica cinerea* L. The inflorescence of the Galway plant is much longer and finer than that of the British plant; about Roundstone it was particularly handsome. At Key Downs 1 a form with very large flowers was seen.

1695. *E. Tetralix* L. On the Lizard Downs 1, a very small flowered form was noticed.

Erica Tetralix × vagans nov. hybr. Last year Mr. F. H. Davey, the very efficient leader of the party through Cornwall and the author of an excellent *Flora of Cornwall* (published J. of B. 333, 1910), the description of a new hybrid heath, which had been found by the eminent horticulturist, Mr. P. D. Williams, of Lanarth, on the downs near St. Keverne 1, as *E. vagans* × *cinerea*. On the second visit Mr. P. D. Williams brought some fresh specimens which the writer considered showed evidence of *Tetralix* as a parent. As it was desirable to see the living plant (a solitary bush) in its native habitat, Mr. Williams kindly motored Professor Graeber, Professor Schroeter and the writer first to his beautiful grounds, where he has a plant in cultivation, next to the plant *in situ*. A careful examination of the plant and its surroundings induced all three botanists to agree that the hybrid must be *E. Tetralix* × *vagans* and not *cinerea* × *vagans*, since the presence of the glandular hairs must have come from the former species.

The longer stamens, the inflorescence and the habit, suggested the presence of *vagans*, both species being in the immediate vicinity.

Planta suffruticosa, ramosissima, 40 cm. alta. Floribus axillaribus vel interdum subterminalibus, in tense roseus, urceolatis, staminobus vagante similibus, sed inclusis, stylis prolongates.

Foliis linearibus, marginibus recurvatis, prope hispido-ciliatis; ovariis hirsutis. I have named it (*Gard. Chron.*, Dec. 2nd, 1911) × *E. Williamsii* after its discoverer. It has been independently described in the *Kew Bulletin*, 1911, p. 378.

1696. *E. Mackayi* Hook. was in good flower at its classic locality, Craigga More, Co. Galway. The glabrous fruit appears to be a constant character.

1697. *E. ciliaris* L. Abundant on a damp heath near Perranwell.

E. ciliaris × *Tetralix*=*E. Watsoni*, Benth. An obvious intermediate, almost certainly this hybrid, growing with both parents in the same locality.

1704. *Boretta cantabrica* O. Kuntze (=*Dabeocia polifolia*). The profusion of this beautiful species at Roundstone greatly rejoiced the foreign visitors, as did the extensive sheets of *Erica vagans* in Cornwall.

1707. *Pyrola rotundifolia* L. var. *arenaria* Koch was still in flower in small quantity at Southport, but building operations and the golf have sadly restricted its area and indeed threaten its existence.

1713. *Limonium vulgare* Miller in various forms and as var. *pyramidale* Druce grew at Havant, Hants, S. 11: the hybrid with *L. humile* (*L. Neumanni* C. E. Salmon) also occurred.

1716. *Limonium reticulatum* Miller, *L. humile* Miller and *L. binervosum* C. E. Salmon were all found in good condition at Blakeney 28, the latter in two modifications.

1714. *L. humile* Miller was also seen at North Bull 21, Ireland, and at Havant, Hants, S. 11.

1722. *Statice maritima* Mill. (=*Armeria maritima*) at North Bull, Co. Dublin. The common plant on Ben Lawers was an alpine form of *S. linearifolia* Laterr., not as has been suggested (Williams *Alp. Fl. Brit.*) *S. alpina* Poiret. *S. linearifolia* was also the common coast plant at Blakeney, Norfolk, W. 28, Southport 59, Dublin, Roundstone, Galway, and the Lizard, Cornwall 1. [This latter plant differs in the spaces between the ribs of the fruit-calyx, being destitute of hairs, which are confined to the ribs only. In true *maritima* the hairs occur also between the ribs, a character which was used by their monographer Boissier to divide the Thrifts into Pleurostichous and Heterostichous groups. In Britain, however, the characters are not very sharply defined. But experimental culture of these forms is sadly needed, and as the distribution of the Thrift is a very interesting one, the results of careful culture and investigation could hardly fail to be of great value.]

1733. *Lysimachia vulgaris* L. with more downy leaves than usual in the Norfolk Broads 27.

1749. *Ligustrum vulgare* L. var. or forma *prostrata*,† Lizard 1, Dr. Ostenfeld.

1765. *Gentiana campestris* L. as the type plant was seen on Lawers 88 and the var. *baltica* (Murbeck) at Southport 59.

1811. *Pneumaria maritima* Hill (*Mertensia*) was pointed out to the party by Professor Oliver on the shingle at Blakeney Point, in its most southern station in England 28.

1854. *Atropa Belladonna* L. In great quantity near Haweswater, Silverdale 69. Probably native.

1878. *Linaria repens* Miller. Plentiful by the railway near Riccarton Junction with *Senecio viscosus* L.† Roxburgh 80. A plant which, like its relation *L. minor*, is spreading along the railway systems.

1903. *Digitalis purpurea* L. As Professor Balfour pointed out that the plants of Ben Lawers are truly perennial, as is the case with those cultivated in the Edinburgh Botanical Garden.

1912. †**Veronica Anagallis** L. The true plant, which differs from the common British plant *V. aquatica* Bernhardi by having bluish petals, by the racemes being longer and with more numerous flowers and the flowers with ascending pedicels, was seen in ditches on the Southport Dunes, Lancashire 59, and has also been gathered by the writer near Galway and on Hampstead Norris in Berkshire 22. It occurs with the upper part of the stem glabrous or glandular; the latter is the var. *anagalliformis* (Boreau). *V. aquatica* Bernhardi has flowers usually white with pink veins, the flowering racemes are shorter with less crowded flowers, and with the flower pedicels nearly horizontal, the fruits are somewhat broader and shorter. This was seen at Cambridge 29, Norfolk 27, 28.

1940. *E. scotica* Wetts. Professor Wettstein confirms Professor Schroeter's determination of "*Euphrasia scotica*" from Ben Lawers as *E. minima*, an opinion independently arrived at by Dr. Ostenfeld.

1944. *Euphrasia salisburgensis* Funck sparingly near Roundstone 16, abundant near Ballyvaghan, Co. Clare 9.

1948. *Bartsia Odontites* Huds. The only form noticed in Norfolk 27, 28, Derby 57, Lancashire 59, Westmoreland 69, Cumberland 70, Perth 87, 88, 89, and in Galway and Kerry was *Odontites serotina* Bertol.

1956. *Rhinanthus Drummond-Hayi* Druce was gathered on Ben Lawers 88.

1968. *Orobanche Hederae* Dubry., Mallow, Killarney: at the latter place also as an albino form.

1960. *Melampyrum pratense* L. var. *hians* Druce. This beautiful form of the common Cow-wheat occurred plentifully in Honley Old Wood, York †63, and also most profusely at Killarney. This plant was unknown to the foreign visitors and it was considered by Professors Graebner and Schroeter to be a well marked subspecies.

[At Keswick the writer noticed that ants were carrying the wheat-like seeds about the wood in which the plant grew.]

1977. *Utricularia intermedia* Hayne. This was fairly common near Sutton Broad, Norfolk, E. 27, and was extremely abundant and luxuriant near Roundstone 16, where it was associated with *U. minor* L., but the new British species *U. ochroleuca* was not observed. The non-occurrence of the latter strengthens the view that it is a species, not a hybrid, since at Roundstone, *intermedia* and *minor* grow inextricably interlaced.

1992. **Mentha crispa* L. near Perranwell, Cornwall 1 quite naturalised: is it not *M. rotundifolia* × *spicata*?

1993. *Mentha piperita* L. Clifden, Galway. Near Kirkland, Cumberland 70.

1994. *M. aquatica* L. var. *minor* Sole. Under this variety comes a very small pretty prostrate form with capitate inflorescence which is abundant in the slacks of the Southport dunes† 59. It may be worthy of a distinct varietal name.

1996. × *Mentha verticillata* L. var. *elata* Host. †Penrose 1. var. *plicata* (Opiz.) †Penrose 1.

1999. *M. rubra* Sm. By the Tay at Perth 89.

2000. *M. arvensis* L. With the above 89.

2062. *Galeopsis Tetrahit* L. A white-flowered form occurred by the Tayside, E. Perth 89.

2099. *Plantago major* L. †var. *pubescens* Lange, Southport 59.

2101. *Littorella uniflora* Aschers. In abundance and barren at Killarney as the forma *isoetoides* Bolle: also at Haweswater 69.

2124. *Chenopodium album* L. Near the var. *glomerulosum* Reichb. Blakeney †28, and Greenfield, York †63.

2143. *Atriplex littoralis* L. Common on the embankment connecting Hayling Island with the mainland. Only the entire-leaved form was noticed.

2144. *Atriplex patula* L. Near Pilgrim Bridge, Lancashire 69 var. Blakeney 28. At Hayling Island 11 var.

2149. *A. Babingtonii* Woods. Blakeney 28, Dog's Bay, Galway.

2152. *Atriplex Portulacoides* L. (*Obione Portulacoides*). In two different modifications on the Blakeney marshes 28, one with paler inflorescences than the other and with narrower leaves. At Havant 11.

2157. *Salicornia lignosa* Woods. Abundant in many places in the north and west of Hayling Island 28. Often associated with the unnamed form of *S. europæa* referred to below.

2159. *Salicornia europæa* L. A distinct form of this species was gathered by Ostenfeld, Lindman and the writer at North Bull, Co. Dublin 21. An allied form grew at Galway 16. Typical examples of the species were gathered at Hayling Island, growing on the landward edge of the association of *Spartina Townsendi*. A variety or allied species was also seen in the same locality, characterised by extremely long, tapering, and often branched spikes, with the lateral flowers of the cyme often separated by the central one as in the perennial species. This form usually grows on the landward limits of salt-marshes.

2160. *S. ramosissima* Woods. North Bull, Co. Dublin 21, The Lizard 1. Locally abundant and characteristic in tidal ditches on the north shore of Hayling Island.

2161, bis. *S. disarticulata* Moss, Journ. of Bot., June, 1911.

This newly described species was rather common in the general salt-marsh association to the north of Hayling Island. It is easily distinguished by its short and uniflorous "spikes."

2164. *Dondia fruticosa* Druce (*Suæda fruticosa* Forskal). Shingle of Blakeney, in magnificent growth, nearly at its most northern station in Europe.

2166. *D. maritima* Druce (*Suæda maritima*). Both in the erect and prostrate (var. *procumbens* Druce) conditions at Hayling Island; also a procumbent large seeded form with seeds ripening earlier which is probably the var. *macrocarpa* moquin.

2171. *Polygonum Bistorta* L. In meadows by the Teith Callander †87.

2200. *Rumex obtusifolius* × *nemorosus*=*R. Dufftii* Hausskn. Monsal Dale †57. Greenfield, York †63.

2207. *Rumex maritimus* L. Near Sutton Broad 27.

2210. *Rumex Acetosella* L. var. *angiocarpus* (Murbeck). The common plants of the British Isles. Noticed at Greenfield, York 63, Southport, Lancashire 59, near Penrith, Cumberland 70, near Whitbarrow, Westmoreland 69, Dunkeld 88, Perth, and at Perranwell, Cornwall 1.

2210. *Rumex Acetosa* L. var. *acetoselloides* (Bal.). Grew on Chewbrook Clough, above Greenfield †63, near the New Reservoir, pointed out by Dr. Ostenfeld.

2219. *Euphorbia hyberna* L. Common in fruit at Killarney.

2245. *Ulmus glabra* Miller. Tall trees nearly 100 feet high at *Mallow †5, *Killarney †2, *Callander †87. Probably planted in these localities.

2246. *U. stricta* Lindley. Near *Gort, Galway †15, Perranwell, etc. 1, near Beaulieu, etc. †11.

2246. *Ulmus hollandica* Miller. *Meltham †63, Mallow †5, Killarney †2, near Cork.

2247. *Humulus Lupulus* L. Near Clifden, close by a cottage, Galway *†16.

2255. *Betula alba* L. (*B. verrucosa* Ehrh.). Plentiful near Honley 63, seen in Silverdale 69, Dunkeld 88, Aberfeldy 89, Trossachs 87, Killarney 2. But with this birch and *B. pubescens* were very numerous trees which could not be referred to either species. Some of these, as at Westwood 63 and Killarney, are probably true hybrids (*B. alba* × *pubescens*), but in addition there are several well marked varieties including *B. pubescens* Ehrh. var. *parvifolia* (Wimm.) and var. *carpatica* W. & K. and another distinct looking tree which is common at Killarney and is perhaps somewhat nearer to *B. verrucosa*. *B. pubescens* Ehrh. occurred near Woodbastwick 27, at Foulshaw Moor 69, Dunkeld 89, Aberfeldy 88, Trossachs 87.

2267. *Salix pentandra* L. In several localities near Clifden, Galway, but perhaps originally introduced.

2272. *S. daphnoides* Vill. var. **pomeranica** (Willd.). Planted doubtless near Southport 59. Professor Graebner named it as the above.

2276. *S. aurita* × *cinerea*=*S. lutescens* A. Kerner. Several bushes of this were seen in the Wessenden Valley, Yorks. †63, also near Dunkeld, Perth E. 89, and at Clifden, Co. Galway.

2291. *Populus nigra* L. Norfolk †27, †28, Meltham *†63. Large trees near Mallow †5.

2293. **P. canadensis* Mœnch=? *P. deltoides* Marsh. The common Black Italian Poplar. Commonly planted through England, South Scotland, and occasionally in Ireland as at Gort, near Limerick, etc.

2294. **P. candicans* Aiton. Planted at Greenfield *63, Southport 59, near Clifden, Galway *16.

2294 (3). **P. laurifolia* Ledel. Some suckers of this alien species were noticed at Woodsome Hall, York. 63.

2308. *Spiranthes spiralis* Rich. In great profusion at Roundstone 16, and at Ballyvaghan, Clare 9, and at the Lizard, at Perranwell 1 and Plymouth 3.

2315. *Helleborine palustris* Schrank. Southport Dunes in abundance, probably as the †var. *ericetorum* (Asch. & Graebn).

2316. *H. media* Druce. Monsal Dale 57.

2319. *H. atrorubens* Druce. Ballyvaghan, Co. Clare 9. A distinctly calcareous species.

2327. *Orchis maculata* L. var. *præcox* Webster. This was still in flower on August 8th in Crowden Clough 58. Comparative culture of this variety or species and the type is greatly needed, especially from seed. But it would be interesting to see what would happen if tubers of the type were grown in acid peaty soil, and those of *præcox* (*ericetorum*) in basic soils. The latter is the prevailing "*O. maculata*" of moors and heaths, the former of woodlands and pastures on basic or neutral soils. Where the soils are variable many intermediates occur, the question to be settled is whether these are natural hybrids, or soil-variations. At Ballyvaghan *O. maculata* var. *O'Kellyi* Druce, a pure white flowered plant with unspotted leaves and narrow lip divisions was over flower.

2341. *Habenaria intacta* Benth. Some fruiting spikes of this interesting plant were gathered in Co. Clare by Mr. Praeger, in this outlying area of its distribution where it is locally abundant. It flowers in June, the blossoms being usually greenish-white, not pink as figured in *English Botany*.

†**Tritonia crocosmiflora* Nicholson Gard. Dict., IV, 94, 1889. (*Montbretia crocosmæflora*=*Tritonia Pottsii* × *T.* (*Crocosmia*) *aurea*). This popular garden plant is becoming naturalised in Ireland. It is quite established near Clifden and Dr. Glück saw it near Ballynahinch. It also grew on the shores of Galway Bay 16, Killarney 2, and as a garden outcast it occurred near Carclew, Cornwall 1.

2390. **Asphodelus fistulosus* L. This European species was noticed by the writer on waste ground in Cambridge †29 and also on the shores of Galway Bay †16.

2426. *Juncus maritimus* Lam. At the back of the salt-marshes, Stiffkey, Norfolk. By the fresh-water stream above Kynance Cove 1.

2428. *Juncus conglomeratus* L. A very much scarcer plant in most districts than *J. effusus*, but typical specimens were seen at Dunkeld, near Roundstone and at Killarney.

2429. *J. effusus* L. was very abundant in most of the districts visited especially at Crowden Great Clough 58, Blackchew 59 and on Crossfell 70. In both places it was associated with the var. **compactus** Lej. & Court., having more compact inflorescences, thus simulating *J. conglomeratus*, but a careful attention to the striation of the stem and the shape of the capsule, easily enable the two species to be distinguished.

2433. *J. subnodulosus* Schrank was plentiful in the area of the Norfolk Broads and appears to prefer basic soils.

2435. *J. articulatus* L. var. *nigritellus* (D. Don) Southport 59.

2437. *J. bulbosus* L. var. *Kochii* (Schultz) Druce. Southport 59, Foulshaw 69, The Lizard 1, Roundstone, Galway. Usually this variety has six stamens but forms with four also occur; its upright habit distinguishes it from the type. The form *fluitans* also occurred in many of the Irish streams.

2440. *J. Gerardi* Lois. Common on the salt-marshes of the coast of Norfolk 28, Lancashire 59, Westmoreland 69, Dublin and Galway.

2441. *J. tenuis* Willd. This aggressive American species which is found yearly in new localities through Central Europe, was gathered on the road-side near Lawers 88.

2442, bis. †**J. ranarius** Perr. & Song. Nees in Linnæa XX, 243, 1847. (*J. bufonius* var. *ranarius* (Nees)). In the damp hollows of the sand-dunes at Southport 59. Professor Graebner says it is an analogous plant to *J. Gerardi* and bears the same relation to *bufonius* as the latter does to *compressus*. It keeps its characters of the shorter and broader capsules and of the shorter perianth-segments, etc. in cultivation. I collected it at the North Bull, Co. Dublin 21. [Mr. Travis also sends it me from Ainsdale, Lancashire 59].

2452. *Juncoides pilosum* Morong (*Luzula pilosa*). Ascending to over 2,200 feet on Ben Lawers, but with a different facies from the lowland plant.

2462. *Sparganium neglectum* Beeby. Silverdale 69.

2465. *S. natans* L. (*S. affine* Schnitz.) at the Trossachs 87, and with *S. minimum* Fries occurs in Loughs near Roundstone.

2476. *Alisma Plantago-aquatica* L. var. *latifolium* Kunth. Near Woodbastwick †27.

2477. *Echinodorus Ranunculoides* Engelm. Southport 59 var. *repens* (Davies) Killarney.

2479. *Sagittaria sagittifolia* L. with extremely narrow aerial leaves in the Broads, as at Barton, and Hoveton 27.

2485. *Potamogeton natans* L. × *P. polygonifolius* (Pourr.= *P. gessnacensis* Fisch.=*P. polygonifolius f. linearis* Syme). This plant grew in great abundance in the Swift Stream (Upper Range) between the Upper and Middle Lakes at Killarney, where it seems to be always sterile. The consensus of opinion expressed by those who saw it was that it was a sterile state of *P. natans*.

2486. *P. polygonifolius* Pourr. This was seen as the heath state near Perranwell (where it simulated to some degree *P. coloratus*) Cornwall, at Dunkeld, and as a very narrow-leaved form at Craigga More, Galway.

2489. *P. alpinus* Balb. Occurred in Loch na Chat, Lawers and also close to Lawers Pier, Mid-Perth.

2493. *P. gramineus* L. (*heterophyllus*) Roundstone.

2503. *P. crispus* L. var. *serratus* (Huds.). Butterston Loch 89.

2508. *P. pusillus* L. As a small form at Roundstone.

2520. *Zostera marina* L. var. *angustifolia* Horn. Hayling Island with 2521 *Z. nana* Roth.

2525. **Aponogeton distachyum* Thunberg. An African species quite naturalised in a small Loch in the Dunkeld policies, E. Perth †89, where it was doubtless planted.

2526. *Eriocaulon septangulare* With. Extremely abundant in Connemara, and also occurring as a land form (forma *terrestris*) at Roundstone. Professor Glück is cultivating this form with a view to determining its status.

2552. *Rhyncospora fusca* Aiton. Very abundant about Craigga More, Galway.

2561. *Carex vesicaria* L. Near Dunkeld by Butterston Loch, Perth, E. 89, Banks of the Teith, Callander, Perth, W. 87, also a hybrid with *C. inflata* Huds. i.e., *C. Pannewitziana* Figg.

2565. *C. lasiocarpa* Ehrh. (*C. filiformis*). Marsh near Butterston Loch, Perth, E. 89.

2570. *C. helodes* Link. Near the Upper Lake, Killarney.

2576. *C. lepidocarpa* Tausch. Sutton Broad 27.

2577. *C. Œderi* Retz. Southport dunes 59, and also in the Norfolk Broads 27, in the latter place as a tall slender form, the var. *elatior* (And.)

2581. *C. ornithopoda* Willd. Monsal Dale 57, gathered by Dr. Ostenfeld.

2600. *C. elata* All. (*C. stricta* Good.). Abundant in the area of the Broads, sometimes forming large tussocks.

2639. **Setaria viridis* Beauv. Casual at Galway †16.

2642. *Spartina alterniflora* Lois. A local patch of this was seen at Warsach on the Hamble Creek, Southampton Water.

2643. × *Spartina Townsendi* Groves. The immense masses of this aggressive form on the tidal mud, Hampshire Coast, was one of the most striking features from an ecological point of view, seen during the expedition.

2644. *S. stricta* Roth. is comparatively rare. North shore of Hayling Island, in company with *S. Townsendi*, which is dominant there as nearly everywhere else on these Hampshire coasts.

2684. *Agrostis alba* L. var. *stolonifera* (L.)=*prorepens* Koch. Southport 59, etc., North Bull, Co. Dublin.

2686. *A. setacea* Curtis. Plentiful on the Lizard heaths.

2709. *Deschampsia cæspitosa* Beauv. var. *alpina* Gaud. Ben Lawers 88.

2724. *Arrhenatherum tuberosum* (Gilib.) Druce (*A. avenaceum* var. *nodosum* Reichb.). Westwood, Yorks 63, Silverdale 69.

2741. *Koeleria britannica* (Domin). Silverdale †69, Roundstone Galway 16.

2745. *Molinia cærulea* Moench occurred with a peculiar interrupted inflorescence at Crowden Clough 58 and as the var. *depauperata* (Lindley) Blackchew 63 and on the moors near Craigga More, Galway.

2759. *Poa pratensis* L. an excellent var. *subcærulea* (Sm.) at Ballyvaghan.

2761. *P. trivialis* L. occurred on Ben Lawers in a peculiar form which is worth further study.

2762. *P. nemoralis* L. var. Killarney.

2769. *P. annua* L. as var *varia* Gaud. On Ben Lawers also as a strong perennial form.

2785. *Festuca rubra* L. This widely distributed species occurred in many forms, at Southport 59 probably as *arenaria* Osb., at Clifden and Roundstone probably as the var. *pruinosa* (Hackel), on Ben Lawers as the var. *megastachya* Gaud. and *barbata* (Hackel).

This grass in its various forms should be well studied by ecologists so that they may know it from forms of *F. ovina* L.

2787. *Festuca ovina* L. Over the greater part of Britain this is doubtless a rarer grass than *F. rubra*, with which it is much confused, but it is an abundant species on the chalk and limestone downs. On the peat moors it is often represented by the variety *paludosa* Gaudin (*F. tenuifolia* Sibth.) an awnless plant, and perhaps a good biological species. In recording *F. ovina* it is extremely important that the species should be authentically named, and also as to the special variety which occurs.

2818. *Brachypodium sylvaticum* Roem. & Schult. On the limestone at Ballyvaghan 9, this assumed much of the habit of *pinnatum*; it occurred also in the var. *glabrescens* Syme.

2827. × *Agropyron Hackelii* Druce (=*A. junceum* × *repens*=*A. acutum* auct. ang.=*Triticum acutum* auct. ang.). This hybrid grass was found near Blakeney 28 in small quantity, at Southport 59, but these much nearer *A. junceum*, and at North Bull, Co. Dublin. At Blakeney a possible hybrid *A. pungens* × *repens* also occurred.

2828. *A. pungens* Roemer & Schult. This grass likes a stiffer soil than *junceum*, which is a plant of mobile sands, while this occurs on the borders of clayey salt-marshes. It was seen near Blakeney 28 and at Havant 11.

2830. *Agropyron repens* Beauv. var. An abundant and dominant plant in the grass vegetation bordering on the salt-marshes at Hayling Island, and especially near Burlesden Bridge, S. Hants; preferring shelter. The leaves are intensely glaucous. [The same form occurs near Boston, Lincolnshire.]

2160. *Juniperus communis* L. Common above Dunkeld, E. Perth 89 and near the Trossachs, W. Perth 87. In each place some forms approaching the so-called variety *coronata* occurred. Bow Hill, W. Sussex.

2861. *J. sibirica* Burgs. (=*J. nana* Willd.). Abundant on Urrisbeg, Co. Galway and descending to near sea-level.

2862. *Taxus baccata* L. Abundant on the limestone of Silverdale, where its luxuriance on a very dry looking limestone scree surprised some of the foreign visitors. Abundant in the Killarney woods. On the chalk of East Sussex and S. Hants, where it sometimes forms pure woods of considerable extent.

2874. *Equisetum variegatum* Schleicher. Southport 59.

2877. *Adiantum Capillus-Veneris* L. In great beauty in fissures of the limestone at Ballyvaghan, Co. Clare 9: the form with large pinnæ.

2880. *Asplenium marinum* L. In splendid condition near the Black Head, Co. Clare and also occurring at the Lizard, Cornwall 1. At the Lizard it grew close to *A. Adiantum-nigrum* and near by occurred a remarkable form intermediate in character suggesting the hybrid, *A. Adiantum-nigrum* × *marinum*. Professor Graebner and Dr. Ostenfeld were also of this opinion, but Dr. Stansfield considers it an abnormal form of the Black Splesmont.

2885. *Asplenium acutum* Bory. Sparingly but in fine condition near Killarney and apparently a distinct species.

2893. *Polystichum aculeatum* Roth var. *lonchitioides* Deakin. Ballyvaghan, Co. Clare †9.

2900. *D. æmula* Kuntz at Killarney plentiful.

2907. *Polypodium vulgare* L. var. *semilacerum*, Mallow.

2916. *Hymenophyllum tunbrigense* Sm. and *H. peltatum* Desv.

abundant at the Trossachs 87 and at Killarney. A carpet-like sheet consisting almost entirely of *H. peltatum* 3 feet long by 18 inches was cut from a rock (where there was great abundance of it) for a museum specimen by Professor Schroeter.

2922. *Pilularia globulifera* L. Killarney. "Sparingly at the south end of Upper lake" *Cybele Hibernica.* This year with the lower water level the shore of the lake and of some stretches of the Upper Range were covered with a turf of this species; the different more yellow-green colour contrasting with similar expanses of *Littorella*, which were also exposed this year from the same cause.

2923. **Azolla caroliniana* Willd. In great abundance and fruiting freely near a garden at Woodbastwick, E. Norfolk 27, and also plentiful in brackish water near Queenstown Junction, Co. Cork 5, having spread from Mr. Beamish's adjoining garden.

Incomplete as the foregoing account of the floristic results of the International Phyto-Geographical Excursion of 1911 avowedly is, yet it contains much that is exceedingly interesting to the student of the British flora, while it emphasises the importance and desirability of more combined and critical work at the constituents of our flora than British botanists have hitherto given, and at the same time shows that even the more frequented areas have not yet yielded all their floristic secrets.

It may be desirable to give in fuller detail the actual additions to the British flora which were made on the expedition, bearing in mind, however, that in some instances the plants had already been distinguished, but not by the more correct name. Other cases are awaiting the results of a more complete examination.

Additions to the British Flora.

77 (2). *Castalia alba* Wood var. *candida* (Presl). Syn. *C. candida* Schinz & Thellung, Fl. der Schweiz, 1909. *Nymphæa candida* Presl, J. & C., Delic. Prag. 224, 1822. *N. alba* var. *oocarpa.* Caspary in Ind. Sem. Hort. Berol. App. 27, 1855. *N. alba* var. *candida* Borbas Buda Korn. Nova 191, 1879.

The description (abbreviated) from that given by Conard *Waterlilies* 172-3, t. 20-22, 1905, is as follows:—

Flower 6-13 cm. *Sepals* 4-5 oblong or ovate-oblong (3-8 × 1-3 cm.) narrowed at apex, acute or obtuse, about 7-veined, green outside, white within. *Petals* 12-20 white, nerved, outer ones nearly as long as sepals. *Stamens* 32-70, shorter than in *alba*, orange yellow, filaments lanceolate (outer) to linear-lanceolate (inner), long acuminate, never narrower than anthers, usually inserted only on the sides, not on the summit of the ovary. *Pollen* granulate with smooth operculum, larger than in *alba. Ovary* ovate or roundish, usually contracted *and destitute of stamen insertions below the stigma. Carpels* 5-14. *Fruit* ovoid or spherical. *Seed* larger than in *alba*, ellipsoid, brownish, 0.3 cm. long. *Leaf* cleft at base to petiole, sub-orbicular to oval, 10-30 cm. long, 25cm. wide, entire, lobes nearly equal, inner margins curved overlapping a little above, and spreading out towards periphery of leaf (or straight and parallel or touching), angles more or less acute. *Veins* on underside of leaf persistent, the lowest pair (*i.e.* those running into the lobes) curved and if produced would cross inclosing an *oval* area.

Loch, Dunkeld, E. Perth, Dr. Ostenfeld. Loughs, Craigga More and Roundstone, Galway, Ostenfeld and Druce.

399. *Sagina nodosa* Fenzl var. *monilifera* Lange. See Ascherson and Graebner, *Flora des Nordostdeutschen Flachlandes*, 30 and 843, 1898.

In this plant the leaf-axils of the lateral stems develop fascicles of small leaves, which drop off and readily take root in suitable conditions. This peculiar modification seems to be more readily induced in bare wind-swept places and the writer has in his herbarium illustrative examples from Braunton Burrows, N. Devon 4; North Warborough, Hants 12; Marcham, Berks 22; Port Meadow, Oxford 23; Near Yarmouth, Norfolk E. 27; Barmouth, Merioneth 48; Aberfraw, Anglesey 52; Southport, Lancashire 59, Portumna, Clare, Galway, North Bull, Dublin and Gweedore, Donegal.

403 (2). *Sagina glabra* Koch Syn. 439, 1842 var. *scotica* nov. var. Ben Lawers, Mid-Perth 88.

Planta elongata, foliis filiformibus, subaristatis, axillaribus fasciculatis, pedunculis solitariis pubescentibus cernuis, petalis calyce duplo longioribus. Habitu laxo, extenso floreque magno, folia omnia elongata.

The above plant differs from *S. saginoides*, with which it has been confounded, by the more creeping growth, longer petals and smaller capsule. The subligneous root stock and creeping-decumbent habit distinguish it from *S. subulata*, while the pentamerous flowers and long petals separate it from *S. procumbens*. From typical *S. glabra* the above plant differs by its smaller and slightly shorter capsules. Professor Graebner thinks my suggestion as to the name it shall bear a very probable one, but we await Professor Schroeter's report on his examination of it with much interest.

The writer has a similar plant from Glen Callater, S. Aberdeenshire, and others exist in the Herbarium at Oxford, labelled *S. Linnæi* from Ben Lawers, and a sheet of it collected from the same mountain by Professor Babington at Cambridge was first labelled *S. procumbens* and then altered to *S. saxatilis* (=*S. Linnæi*=*S. saginoides*).

488 var. *Geranium Robertianum* L. var. *villarsianum* (Jordan in Cat. Grenoble, 1849) as a species=*G. purpureum* Vill. Fl. Dauph. iii., 374, t. 40 pro parte. This differs from *G. modestum* and *G. purpureum* by its prostrate growth, by its smaller size, its usually green flattish leaves and slight odour. Specimens from the calcareous district of Ballyvaghan are almost identical with Jordan's type, which by the kindness of Dr. Moss I have been enabled to examine in the Cambridge Herbarium. Jordan's description is appended:—

"G. pedunculis bifloris, inferioribus folia vix æquantibus, sepalis dense glanduloso-hispidis dorso *convexis* late costato trinerviis latiuscule membranaceo-marginatis aristatis, petalorum limbo parvo læte purpureo *oblongo-obovato* unguem suum fere a basi anguste alatum *æquante*, antheris flavis orbiculato-bilobis stigmata pallide purpurea vix æquantibus, fructus rostro 4-5 lin. (10-12 mm.) longo, carpellis *mox deciduis* rubellis glabris *dense* rugoso-costatis, rugis superioribus transversalibus *crassis approximatis* vix apice ramulosis, inferioribus obsolete areolatis vel subverticalibus, semine parvo ovoideo lævi, foliis parvis intense virentibus crassiusculis planis circumscriptione rotundato-pentagonis subquinatis, partitionibus petiolulatis ovatis profunde pinnatifidis, lobis *paucis* distantibus obtusis mucronulatis integris vel subdentatis, caule humili erecto simplici vel diffuse-ramoso, ramis ascendentibus undique patenter glanduloso-villosis, radice bienni.

Hab. in locis saxosis et rupestribus montium calcarearum. Caulis vix ultra sex pollices altus, odor lævis.

A *G. Robertiano* plane differt floribus duplo minoribus, carpellis magis rugosis, foliis parvis minus dissectis et fere crassioribus, habitu valde humiliore diffuso.

A *G. modesto* Jord. discedit sepalis multo longius pilosis magis dorse convexis, petalis latioribus minus oblongis ungue suo haud longioribus fructu rostro breviore, carpellis mox deciduis nec diutius suspensis, rugis eorum crassioribus, foliis obscure virentibus minus dissectis, hispiditate longiore, habitu humiliore diffuso."

519. *Rhamnus catharticus* L. var. *Schroeteri* nov. var. Silverdale, Lancashire. Arbor parva (3-4m. alta). Foliis ovalibus orbiculis, flave-viridibus, acuminatis (25-30 mm. longis 15-20 latis), supra infraque dense pilosis; petiolis dense pubescentibus; fructus cum pedunculis hirsutis.

The pubescence is of such a nature as to appear mealy, and the whole foliage appeared of a dusty yellowish tint, quite unlike that of the midland plant. Professor Schroeter, who first drew attention to this example, has kindly sent me a specimen of *Rhamnus Villarsii* Jordan, itself more hairy than the type, but he agrees with me in thinking the British plant quite distinct from Jordan's species from Fribourg.

909. *Alchemilla vulgaris* L. var. *acutidens* (Buser as a species) Briquet. We await Dr. Ostenfeld's notes on this plant, which he showed to the party on the ascent of Ben Lawers.

1042. *Peplis portula* L. var. *dentata* nov. var. Killarney, Co. Kerry. This form which was first gathered by the writer in the Black Valley, Co. Kerry, in 1875, subsequently at Boscastle, Cornwall, and again this year with the Excursion, differs from the type in having much longer teeth to the calyx and may be described "Dentibus calycis capsula (1 mm. vel. ultra) longioribus." It forms a passage to the Mediterranean and Western variety *longidentata* J. Gay, and is especially interesting as affording another link with the Iberian flora.

1434. *Cirsium palustre* Scop. var. *ferox* nov. var. Crossfell, etc. This extremely spinous variety was seen in many places on the Excursion and the members agreed in considering it distinct. It may be defined as:—Planta robusta (40-60 cm. alta), pallide viridis, spinosissima, cum pallide-flavis spinis (fortibus). Capitulis pallidis-roseis vel albis; floribus, in densis racemis terminalibus aggregatis. Phyllariis pallidis cinereis-viridibus, externalibus forti spina terminatis, parte media viscida, fulgida subnigra, paucis pilis glandulosis: phyllariis superioribus in apice plane scariosa terminatis.

Doubtless the drought and sunny weather of this abnormal season would tend to reduce the vegetative growth and thus produce a more spinous condition than in wet years, but the characters of this plant appeared to be to some degree independent of these factors. Cultural experiments are however much to be desired, to see if the features of the variety are constant.

1638. *Hieracium umbellatum* L. var. *dunale* G. Meyer. Chlor. Hannov. 421, 1836; var. *armeriifolium* G. Meyer in Hann. Mag. 170, 1824=*H. dunense* Reymer in v. Hall. Fl. Belg. i., 556. Southport Dunes 59, named by Professor Graebner and assented to by Dr. Ostenfeld. Rouy & Foucaud (*Flore France* ix., 401) say this plant is identical with *H. littoreum* Lindberg, not Arvet-Touvet, which is the var. *littorale* from the Jersey dunes.

1693. *Calluna vulgaris* Hull var. *Erikae* Aschers. & Graebn., Fl. Nord, Flachs. 547. 1898-99, where it is defined " B. breit, flach, beiderseits rinnig." Its procumbent form makes it a desirable plant for the rock garden. Dr. Church in his excellent *Floral Mechanisms*, p. 147, describes and figures the inflorescence of this variety, which he found at Cape Cornwall, and shows that visiting insects crawl underneath the plant, between the flowers, which are turned downwards, and the ground. Although more frequent in exposed and windswept places it is by no means confined to them as it often grows with the typical plant.

1695. *Erica Tetralix* × *vagans*=*E. Williamsii* Druce in Gard. Chron., December 2nd, 1911=*E. cinerea* × *vagans* Davey in Journ. Bot. 333, 1910=*E. vagans* × *tetralix* Turrill in Kew Bull., 378, 1911, see preceding page.

1912. *Veronica Anagallis-aquatica* L. em. Asch. & Graebn. Fl. Nord. Flach. 635. 1898-99, diagnosed as " St. aufrecht od. aus liegendem Grunde aufrecht, einfach od. ästig, fast 4kantig; B. länglich-lanzettlich bis lanzettlich, sitzend, halbst. umfassend, entfernt-kleingesägt; Trauben vielbth, etwas locker, zerstreut drüsenha.; Bth.-stiele länger als das Tragb. u der K. in der F. abstehend; Bl.-kr. bläulichweiss, mit dunkleren Adern; Kapsel rundlich.

1912 bis. *V. aquatica* Bernh. This is the common plant of Great Britain and Ireland and is defined by the foregoing authors as:—B. oft röthlich uberlaufen (Scholz); Bth. kleiner; Bl. kr. weisslich-rosa; F.-stiele derber, ziemlich starr, wagerecht abstehend, daher der F. stand sehr locker; Kapselelliptisch." The *Index Kewensis* gives *V. aquatica* Benquerel in Neuch Bull. V. 449, 1859-61.

2429. *Juncus effusus* L. var. *compactus* Lejeune & Courtois, p. Fl. Belg. ii., 23, p. 131. This form, which is often mistaken for *J. conglomeratus*, differs from the type of *J. effusus* by the inflorescence, even at maturity being condensed into a globular head, with the internodes very reduced; but intermediate stages occur.

2442 (2). *Juncus ranarius* Nees in Linnæa XX., 243, 140 (teste *Ind. Kew.*) emend Song & Perrier in Billot Annot. Fl. Fr. et. Allem. 192, 1859. This plant, which in Britain has either been confused with or called var. *fasciculatus* of *Juncus bufonius*, is stated by Professor Graebner to be a good species, a view also held by Buchenau, the monographer of the genus. Ascherson & Graebner (*Fl. Nord. Flach*, 175, 1898-9), thus describe it:—" H. 5-23 cm. Bth. häufig zu 2-3 genähert; innere P-b. etwas kürzer, äussere so lang od etwas länger als die am Grunde deutlich schmälere Kapsel; I have it also from the Lizard, Cornwall 1; Braunton Burrows, Devon

4; Lydd, Kent 15; Yarmouth, Norfolk, E. 27; Tenby, Pembroke 45; Holyhead, Anglesea, 52; Holy Isle, 67; Kinross, Fife, 85; Sands of Barry, Forfar 90; Kishorn, W. Ross 105; Betty Hill, Sutherland 107; North Bull, Dublin; Newcastle, Co. Down.

Four Alien plants not in my *List of British Plants* were also gathered on the Excursion, viz., *Saponaria orientalis* L., an eastern species introduced with other Aliens at Galway Bay: *Populus laurifolius* Ledeb., the remains of cultivation in the Earl of Dartmouth's grounds at Woodsome Hall, near Huddersfield, Yorks; *Tritonia crocosmiflora* Nicholson, a garden hybrid rapidly becoming naturalised in Western Ireland; and the variety of the Violet Willow, *Salix daphnoides* Vill. var. *pomeranica* (Willdenow), which is evidently planted at Southport. The last was identified by Professor Graebner.

G. CLARIDGE DRUCE.

THE ROOTS OF SOME NORTH AFRICAN DESERT-GRASSES.

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[With Plate VI. and Two Figures in the Text.]

THE Grasses whose root structure is dealt with here, all come under a general type, and all live in extreme conditions of aridity in the North African Deserts. A detailed study of the internal anatomy has been possible in one case, that of *Aristida pungens*, while a few other species are considered in relation to this type.

I. *ARISTIDA PUNGENS*, DESF.

Aristida pungens, Desf.[1] grows abundantly in North Africa, and is also distributed in Arabia, Turkestan, Siberia,[2] &c.—that is to say it is a desert grass. The genus *Aristida*, characterised by a three-branched awn of which one branch is plumed, is allied to the genera *Stipa* and *Amphopogon*, and also to *Alopecurus* and *Phleum* of the British Flora, all being included in the tribe Agrostideæ.[3]

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[1] Desfontaine. *Flora Atlantica*, Paris, 1800, Tome I., p. 109 and Tome III., fig. 35.

[2] Index Kewensis, Fasc. 1, p. 187.

[3] Hackel, in Engler's Pflanzenfamilien II., 2, Gramineæ, pp. 44 and 45.

HABIT AND HABITAT.

Aristida pungens is very widespread in the North African Sandy Deserts. In the Algerian Sahara it is characteristic of, and appears to be confined to, the sandy as opposed to the stony desert. In this region the grass is called the "Drin." Massart[1] states that in appearance it somewhat resembles the *Ammophila arenaria* of European dunes and that it is important as a grazing grass in the desert. The peculiar habit has been fairly fully described by Volkens[2] and also by Massart,[3] The roots spread out to a great distance from the stock of the grass, 20 metres being probably far too low an estimate, and maintain a position a few inches below, and more or less following the undulations of the surface of the sand. The roots are thin and cord-like, maintaining a fairly uniform thickness throughout, and surround themselves with a peculiar sheath, composed of agglutinated particles of sand—"wie das Bein in der Hose, oder besser und ästhetischer ausgedrückt, wie eine Phryganeenlarve in dem selbst gebauten Gehäuse." [4] This sandy sheath is fairly hard and resistent, retaining its shape when the root dries up, though it then becomes very brittle : this feature is clearly shown in dried herbarium material. The root-hairs, generally the most ephemeral perhaps of all the organs of a vascular plant,[5] in this species and in a few similar Monocotyledons, do not disappear, but, according to Volkens and Massart, remain throughout the length of the root.

As was to be expected from this characteristic habit the morphology and anatomy of the roots, exhibit features which are interesting in relation to biological adaptation.

The material upon which the present work was carried out was collected by Mr. A. G. Tansley at Aïn Sefra in the Algerian desert while on an expedition during the spring of 1910. The grass grows in abundance on the great sand dunes of Aïn Sefra,[6] but considerable difficulty was experienced in obtaining root-tips owing to the great length of the roots, which were very easily broken in the attempt to follow them to their extremities. The material, which was sparing in quantity, was eventually obtained from small shallow patches of sand away from the dunes themselves; in these the growth in length of the roots was limited, and it was possible by careful digging to obtain the apices at no great distance from the shoots.

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[1] Massart, Jean. Un Voyage Botanique au Sahara. Bull. Soc. Roy. Bot. Belgique, Tome XXXVII., 1898. Especially pp. 237-240.

[2] Volkens. Flora der Ægyptisch-Arabischen Wüste. Berlin, 1887, pp. 25, 26, etc.

[3] Massart, l.c.

[4] Volkens, l.c., p. 26.

[5] Massart, l.c., p. 238.

[6] v. Karsten & Schenck. Vegetationsbilder, 6 Reihe, Heft Taf. 24, Jena, 1908.

METHODS.

Anatomical investigation was difficult on account of the particles of sand forming the sheath and adhering to the outer surface of the roots. The outer layers of sand were easily disposed of, and in most cases had become removed in the processes of collection and transport. Many of the particles adhered firmly, however, so that section cutting was practically impossible without special treatment.

The root-tips themselves were comparatively free from sand except for some very small particles. Attempts were made to clean these by brushing gently with a soft "camel's-hair" brush and after this treatment they were embedded in paraffin and sections were cut with a Cambridge Rocking Microtome in the usual manner. A few fairly good sections were obtained, but in most cases small particles of sand still remained which tore the sections. For the thicker parts of the roots, where the sandy sheath was fully developed, brushing was quite useless.

Silica is dissolved by the action of hydrofluoric acid, and use was made of this reaction. The pieces of root were placed in 95% alcohol and were treated with commercial hydrofluoric acid which was added from time to time.[1] Glass vessels coated with paraffin wax were employed.[2] The pieces when they appeared free from sand were transferred to fresh alcohol and then treated as usual. With the older portions of the root this method was quite successful, and following its use, good sections could be cut, showing the structure of root-hairs, and so on. For the root-tips the treatment was usually too severe. Unless very dilute acid be used, the outer portions, including the root-cap and secretory layer, are more or less completely disintegrated and removed. Using weak acid some sections were ultimately obtained, but the tissues were rather softened and often displaced, though good sections of the secretory layer (*v. infra*) were produced.

With regard to stains, Diamant Fuchsin was good for the mucilage, and was followed by a very dilute alcoholic solution of Licht-

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[1] The fumes of the acid are extremely dangerous and the greatest precautions must be taken when using this method. In all cases above the reactions were performed in the open air.

[2] Bolles Lee, A. The Microtomist's Vade Mecum, 4th edition, London, 1896, pp. 327-8. See also Zool. Anz. 97, p. 593, 1881.

Grün to remove some of the stain from the cell-contents. Gentian Violet, Orange G combinations and Delafield's Hæmatoxylin were also useful.

EXTERNAL MORPHOLOGY.

The roots as already mentioned are long and have an average thickness of about ¼ inch or 6 mm. To judge from the herbarium material branching is very rare, each root being one long cord-like organ. They taper rapidly towards the tip and here there is little sand adhering. The stele forms a small wiry strand, sharply marked off from the wide cortex; the latter can be easily pulled away leaving the stelar strand quite clean. Outside the cortex is the "caddis-worm" case, as it may be fancifully called, and when this has been removed the root-hairs can be seen on the older portions of the root. Hairs seemed to be always present on the older parts of the spirit material, except at one branching knot, evidently of an old root, where hairs were quite absent. Herbarium material examined with a simple lens, shows the hairs persisting right up to the point of origin from the stock. They project only a short distance from the sandy sheath, and probably when this is quite complete they do not emerge from its outer surface.

In dried material, the cortical zone has generally collapsed and almost disappeared, leaving the central stelar strand surrounded loosely by the sandy sheath.

ANATOMY.

In dealing with the anatomy the various tissues are traced backwards from the root-tip to the adult structure.

In general the relation of the meristematic layers to the root-cap is of the so-called "liorhizic type" of Van Tieghem[1] which is characteristic of Monocotyledons. Here the root-cap is quite distinct from the outer layers of the cortex, and is formed by special meristematic cells, lying just outside those which give rise to the piliferous layer of the root.[2] The tissues of the central cylinder on the one hand and of the piliferous layer on the other, apparently arise from separated meristems, much as in the usual Graminaceous type[3] so that it is needless to describe their origin in further detail.

The root-cap is composed of large cells towards the exterior and smaller regularly arranged ones within. The outer cells are markedly mucilaginous, and the mucilage is obviously formed by the swelling up of the cell-walls, with subsequent complete disintegration of the cells (Plate 6, fig. 1). This phenomenon is of course quite normal in root-caps, but probably here the mucilage formation is rather exaggerated.[1]

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[1] Van Tieghem. Traité de Botanique, 2nd edition, Partie I., pp. 696 *et seq*, Paris, 1891.

[2] Van Tieghem, *l.c.*, p. 698, and also Bonnier and du Sablon, Cours de Botanique, Paris, 1901, Vol. I., p. 341 *et seq.*

[3] Flahault. Ann. Sci. Nat. Bot., Sér. 6, tome 6, pp. 20 and 28, 1878.

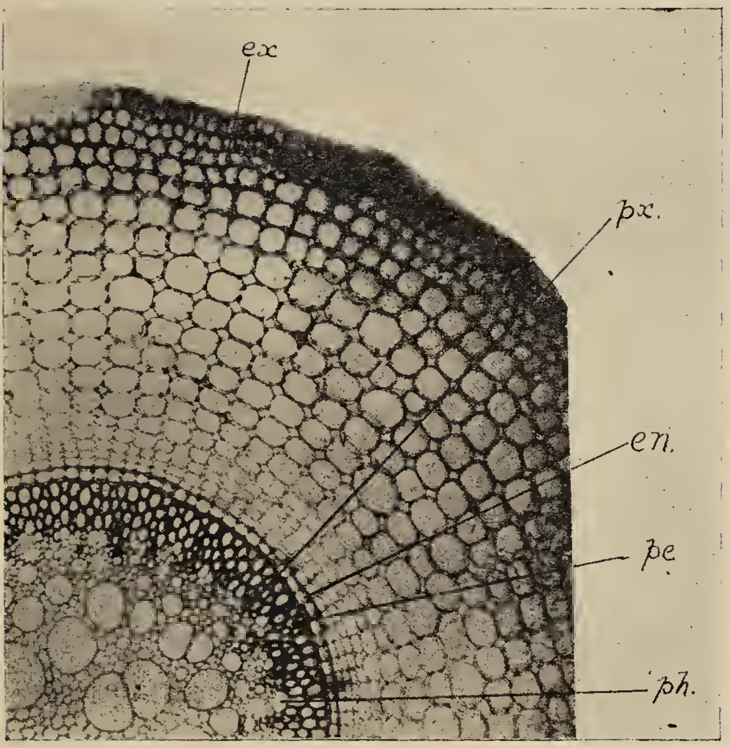
Coming to the root-tip itself, the most striking feature is the character of the cells which compose the outer layer of the cortex—the piliferous layer. This layer is composed of regularly arranged cells, each cell being slightly elongated in a direction perpendicular to the root-surface (Plate 6, figs. 1 and 2). The anticlinal walls are straight and parallel, while the outer tangential walls are rounded or sometimes slightly conical. This rounding of the free wall is evident quite close to the apical meristem. The whole outer layer appears as a regular palisade of cells on the outside of the root. Each of these cells seems to act as a mucilage-secreting gland, the outside of the root being covered by a wide layer of mucilage resulting from the activity of these glands. The cells appear to function thus almost as soon as they are formed, for a thin layer of mucilage extends almost up to the apical cells, between the tissues of the root-cap and root-tip, this layer gradually becoming thicker as we pass away from the apex (Plate 6, Fig. 1).

The mucilage appears to be actually secreted gradually by the cells, and is not formed by the wholesale conversion into mucilage of the outer walls. In some cases the mucilage layer was torn off in cutting (Fig. 4), or removed by hydrofluoric acid, but the glandular cells still retained their contour and showed a perfectly distinct outer wall. It is also noticeable that the mucilage secreted by these cells stains rather more deeply with Diamant Fuchsin than does the mucilage formed by the root-cap cells. The wide layer of mucilage exhibits slightly marked radial striae which correspond to the divisions between the secreting cells. There is also a series of tangential striations which are arranged roughly concentrically with the tangential outer walls of the cells (Figs. 3 and 4). This system of striations may indicate that mucilage formation takes place by the modification and swelling of the *outer portions* of the cell-walls, which are constantly renewed by the protoplasm within the cells—quite a different process from the simple swelling of a wall to become mucilaginous, in that it is continuous and progressive. The activity of these cells is also indicated by their very dense protoplasmic

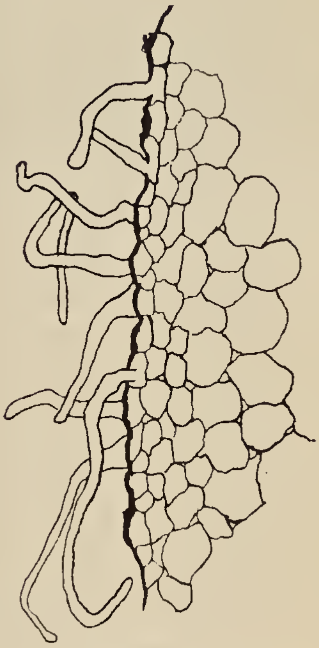
[1] Van Tieghem, *l.c.*, Fig. 458, and also Strasburger, Text-book of Botany, Eng. Trans., 3rd Edn., London, 1908, Fig. 168.

contents, and by the presence of a large conspicuous nucleus in each. The nuclei, whose fixation was very indifferent, are situated rather towards the bases than the apices of the cells (Figs. 2, 3 and 4).

The regularly arranged gland-cells are present for a distance of about ¼-inch (6 mm.), or a little more, behind the meristematic apex, and then seem to pass over gradually into cells of ordinary parenchymatous type, elongated in a tangential direction (Fig. 5).



Text-fig. 1.



Text-fig. 2.

Text-fig. 1. Photograph of part of transverse section of the root of *Aristida pungens*, showing the regular cortex with large lacunæ, the exodermis (*ex.*), the endodermis (*en.*), the wide sclerenchymatous pericycle (*pe.*) with numerous phloem groups (*ph.*) situated in the bays, the alternating protoxylems (*px.*) opposite the projections of the pericycle. × 60 diam. (app.)

Text-fig. 2. Portion of transverse section of a root of *Aristida pungens*, nearly mature, showing the cells of the piliferous layer which have grown out to form short root-hairs. Root treated with hydrofluoric acid. × 102 diam.

Beneath the secretory layer is a zone of thin-walled cells (about two cells thick) with less dense contents, seen especially well in transverse section just behind the root-cap. This probably corresponds to the "exodermis" or cuticularised hypodermal layer, as for example in *Lygeum Spartum* Lof. mentioned below. Within this exodermis is a region of several layers of closely packed cells, and then an inner cortex of regularly arranged cells with large intercellular spaces (Fig. 3).

Just above the position in which the gland cells disappear as such, the tissues of the root reach their full development. A transverse section cut in this region or a little further back, say an inch (24 mm.) from the root-tip, shows a typical Monocotyledonous root structure (Text-fig. 1). The outer layer of the cortex—the piliferous layer—is composed of rather small cells which appear rounded in transverse section. Within this there are one or two layers of rounded cells with no very regular arrangement, forming the exodermis, and this passes over into the inner cortex. The cells here are arranged in a very regular manner in concentric layers and radiating rows, with well-marked intercellular spaces between the corners of the cells, the whole appearing almost diagrammatic in arrangement, as is often the case in Monocotyledonous roots.[1] As usual in such roots the endodermis is well marked. The stele is rather remarkable for a peripheral zone of sclerenchyma, several cells in width and representing the pericycle. On the inner edge of this pericyclic zone are a number of bays, in each of which is a small phloem group. The root is polyarch, with as many as forty protoxylem groups in some cases. The rest of the conjunctive tissue is of a distinctly sclerenchymatous type, though not so thick-walled as the tissue of the pericycle. In the fully mature stele especially there is a well marked central pith, also sclerenchymatous. It is this large development of sclerenchyma which gives the stele its great mechanical strength

Passing to the region where the full thickness is first attained, say 1½—2 inches from the tip, the general structure is practically the same, but now the piliferous layer justifies its claim to the name. Numerous root-hairs of the usual type occur, that is they are simply outgrowths of the outer cortical cells. On the whole the hairs appear less numerous than in the " root-hair region " of a typical young root, but this must be more than compensated for by the very great length of root surface occupied by hairs. Text-figure 2 shows a portion of the outer cortex of the root in this region.

In the region towards the point of insertion on the stock, the root-hairs increase very much in length. Only herbarium material was obtainable of this region, but this when soaked in alcohol and teased out in glycerine, showed the hairs quite well. Fig. 6 is drawn from a portion of material thus treated and shows the long root-hairs.

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[1] cf. Bonnier and du Sablon, *l.c.*, Fig. 512.

As already mentioned, sections of a branching knot which exhibited a structure certainly quite as mature as that from which Text-fig. 2 was drawn, and which were of greater diameter, failed to show any signs of hairs. Otherwise the hairs appear to be quite ubiquitous and persistent.

The processes which take place as one of the roots of *A. pungens* grows through the soil is probably much as follows. The mucilaginous root-cap allows the root to pass easily through the sandy soil and prevents its tip from drying up. The layer of mucilage behind the tip comes into contact with the soil and sand grains are embedded in it. The mucilage gradually spreads round the grains and comes into contact with others, while the root expands. When the root has reached its full diameter the complete sheath formed of sand grains cemented together closely invests it. The cells of the piliferous layer now grow out into the root-hairs which embed themselves in this sandy sheath.

The root-hairs themselves obviously do not secrete the mucilage,[1] but simply serve as absorptive organs in the usual way.

Biologically, this root system seems specially well adapted for obtaining the least traces of water from the arid and very permeable surface soil of the sandy desert, and also it is able quickly to absorb the water resulting from slight precipitation. The roots of a single plant radiate through a large area of the surface sand, and by their special adaptation are enabled to obtain water from all points of this area with which they come in contact. Thus they differ markedly from the roots of ordinary land plants, for these, even if they occupy a large volume of soil, can only absorb water through their tips and the tips of their branches. The intimate relation of sand, mucilage and root-hairs must also naturally promote water absorption. The mucilage itself has a high absorptive power for water, and transfer of water can easily take place in the mucilage system, so that the whole cylinder of sand in the vicinity of the sheath is very completely drained.

The sheath of mucilage and sand also undoubtedly serves another important function—that of protection.[2] In times of intense drought and great heat it is almost certain that the root-hairs would be shrivelled if they extended freely into the sand, and as they are permanent organs it is more than ever important to the plant's economy to prevent this. It is rare for a corky periderm to be formed by a monocotyledonous root, but the mucilaginous sheath is an excellent substitute. The mucilage, which retains water very persistently, must be quite dried before the root-hairs are injured. The sheath will also serve to protect the hairs and delicate cortex from mechanical injury.

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[1] Volkens, *l.c.*, p. 26.

[2] Volkens, *l.c.*, p. 26.

How respiration takes place under these conditions is rather a difficult question, but the intercellular space system is very well developed—far more so than in most desert plants—presumably for gaseous circulation. It is possible that the main interchange of gases with the outer air takes place at the base of the plant stock.

The roots are not positively geotropic, and Massart suggests[1] that the light determines the depth of the root-tip below the surface of the soil.

II. OTHER SPECIES.

The following species were examined as herbarium specimens only. Pieces of the roots were removed, soaked in alcohol, and treated with glycerine for microscopical examination of the root-hairs and the sand particles. In some cases also sections of the wiry steles were obtained, but usually no precise anatomical examination was possible.

ARISTIDA OBTUSA DELILE.

This is also a perennial grass which inhabits the desert regions of Egypt, North Africa, Arabia, &c.[2] In habit it is very much smaller, and more tufted than *A. pungens*, while the roots are smaller and probably much shorter. The herbarium material collected by Dr. Moss and Mr. Tansley in Algeria shows two forms of the species, one with a more open habit than the type, and with pubescent leaf sheaths, the two characters together giving a distinctly different vegetative facies. The distinction does not, however, appear to be specific, and the anatomy of the two forms is closely similar if not identical.

The roots show very much the same type of adaptation as those of *A. pungens*, but this is not quite so pronounced. There is a distinct sandy sheath into which the root-hairs project, and these latter scarcely extend beyond the sheath. Moreover, as in *A. pungens*, the hairs are persistent.

The structure of the stele seems on the whole to be very similar to that already described for *A. pungens*. The sclerised pericycle consisting of several layers of cells is present, though its cells are not so strongly thickened as in *A. pungens.* The external elements of the protoxylems extend to within one cell of the endodermis while the phloem groups are placed in juxtaposition with the "capes" of the pericycle. Thus the arrangement of protoxylems and phloems is rather different from that obtaining in *A. pungens.* There are also some small groups of phloem embedded in the sclerised conjunctive between the larger vessels of the metaxylem. The pith is less thick-walled than in *A. pungens.*

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[1] Massart, *l.c.*, p. 239.

[2] Boisser, "Flora Orientalis," Vol. V, Geneva, 1884, p. 494.

LYGEUM SPARTUM Lofl.

This species—the well-known "Esparto Grass"—grows in the Mediterranean region of Spain, Algeria, &c.[1] A specimen gathered in the Algerian desert was growing on sand, apparently a common habitat of the species.[2]

A distinct sandy sheath was present on the roots in this material, but was not quite so thick or coherent as in *A. pungens.* The root-hairs are short and hardly project at all from the sheath, even in the dried material. They are persistent to within an inch or so of the point of insertion of the root.

The dried material was soaked out in alcohol for some time and then treated with hydrofluoric acid. Microscopic examination before treatment with acid showed the grains adhering closely to the outer surface as in *A. pungens.*

After the sand had been removed, sections exhibited a well preserved structure. The piliferous layer is normal in appearance and within it is a cortical zone composed of four or five layers of cells with very thick walls strongly cuticularised (Fig. 7). In the material thus treated it was not possible to make out any pits or passage cells, but such must exist if the root-hairs are functioning in this region—the latter presumption seeming very probable.

On the whole the rough examination possible seems to point to an adaptation very similar to that in *A. pungens* or *A. obtusa*, but certainly not so well marked as in *A. pungens*, together with a highly developed protective mechanism, in addition to that presented by the sandy mucilaginous sheath, and absent or much less developed in the species of *Aristida*.

BROMUS TECTORUM L.

This species is widespread in Europe and in North Africa, growing on walls, arid places and in the desert.[3]

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[1] Boissier, *l.c.*, p. 452.

[2] Warming, "The Œcology of Plants," p. 284, Oxford, 1909.

[3] Boissier, *l.c.*, p. 647.

The material dealt with here was gathered on the Aïn Sefra sand dunes. The plant is an annual. The roots form a small tuft at the base of the stock, and descend vertically into the sand to a depth of three or four inches. The root hairs are long and persistent, and at first sight there appears to be a sandy sheath. Closer examination of the soaked out material, however, shows that there is no sheath of the type found in the two species of *Aristida*. The grains of sand seem to be held more especially by the long tangled root-hairs which project freely into the sand around. Some grains show a close contact with the outer layers of the cortex, and this fact, together with the large number of grains held, very possibly indicates that a certain amount of mucilage is secreted here, although this was not actually demonstrated.

SCHISMUS CALYCINUS L.

This is also a small annual grass found in the Mediterranean region and in North Africa.[1] The herbarium material shows a spreading habit, with a small bunch of adventitious roots at the base, penetrating the sand to a depth of three or four inches. The root-hairs clothe the whole length of the roots, and are remarkably long. The large amount of sand brought away with each root, appears to be due rather to the entangling of the grains by the long root-hairs than to the presence of mucilage. At any rate there is no attempt at the formation of a definite cemented sheath, and the grains do not seem to adhere to the outer cortex to any extent.

HORDEUM MURINUM L.

What is apparently a sand form of the common barley-grass of waste places was collected from the dunes of Aïn Sefra. The species grows generally in arid places in Europe, North Africa, America, &c.[2] The plant is an annual and the roots are very similar to those of *Schismus calycinus* just described.[3] The root-hairs are very long, and persist throughout the whole length of the root, while sand grains are entangled by these hairs in much the same way.

III. GENERAL CONSIDERATIONS.

From the examples dealt with and also from those mentioned by Volkens,[4] it seems that the persistence of the root-hairs is quite a general feature of the grasses of the sandy desert. Massart mentions this fact for *Aristida pungens*, *A. floccosa*, *Panicum turgidum*, *Pennisetum dichotomum*, *Danthonia Forskalii*, and also states that it occurs with most of the perennial grasses growing in the sand of the desert. From the cases dealt with in this paper it appears that some of the annual grasses with shorter roots also exhibit the same phenomenon. It is obvious at once that this is of advantage to the short-lived species, but in the perennials the freely exposed hairs and piliferous layer would certainly be dried up during the hot dry summer. It thus seems that the adaptation, already dealt with for *A. pungens*, *A. obtusa* and *Lygeum Spartum*, may be a special case of this general persistence of root-hairs, modified to serve the needs of a perennial plant. Some of the cases like *Bromus tectorum* show how the type may have arisen by the increased secretion of mucilage and the confinement of the root-hairs within the limits the sheath so formed.

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[1] Boissier, *l.c.*, p. 597.

[2] Boissier, *l.c.*, p. 686.

[3] cf. Cannon "Root Habits of Desert Plants," Carnegie Instit. Publication, 131, 1911, p. 34.

[4] Volkens, *l.c.*. p. 25.

A. pungens probably represents the most efficient arrangement for obtaining water from the arid soil, in which the permanent underground water supply lies at a very great depth, and exhibits what may be regarded as a well marked "adaptation" to intensely xerophytic conditions. It is almost certainly this adaptation which has enabled the plant to assume a dominant place in the vegetation of the sandy desert.

The type of adaptation may be contrasted with that exhibited by many desert plants, *viz.*, the production of very long roots which descend vertically to the permanent supplies of water far below the surface of the soil.

My best thanks are due to Mr. A. G. Tansley, who suggested the work, supplied the preserved material of *A. pungens* and who has given his advice throughout: also to Dr. C. E. Moss for the use of the herbarium material; and also to Mr. H. H. Thomas for the photograph.

BOTANY SCHOOL,
CAMBRIDGE.

November, 1911.

DESCRIPTION OF PLATE VI.

ALL FIGURES DRAWN WITH THE AID OF A CAMERA LUCIDA.

FIGURES 1—6. *A. pungens.*

Fig. 1. Radial longitudinal section through root-cap and tip of *A. pungens.* Microtomed after treatment with Hydrofluoric Acid. Note the outer cells of

the root-cap with mucilaginous walls (*c*), the layer of mucilage (*m*) secreted by the tissue (*s*). ×405 diam.

Fig. 2. Transverse section through the tip of a root, showing root-cap (*c*), the mucilaginous layer (*m*) between the secretory layer and the cap, and the secretory cells themselves with distinct nuclei. ×405 diam. Brushed and microtomed.

Fig. 3. Transverse section above the root-cap. Note the wide layer of mucilage with faint radiating and tangential striations. The secretory layer (*s*), the exodermis (*e*) and the inner cortex. Root-tip brushed and microtomed. ×405 diam.

Fig. 4. A few secretory cells more highly magnified. Shows the mucilage layer partially freed from the outer cell walls, the dense contents of the secretory cells and distinct nuclei. Treated with hydrofluoric acid and microtomed. ×1000 diam.

Fig. 5. Longitudinal section in region of gradual modification of secretory cells into cells of the piliferous layer. Grains of sand still adhering. ×405.

Fig. 6. Portion of outer cortex soaked and teased out from herbarium material. Quite mature root showing the long root-hairs, with a single sand grain *in situ*. ×102 diam.

Fig. 7. *Lygeum Spartum*. Transverse section showing portion of outer cortex of root in its thick part. The piliferous layer with root-hairs of normal type and the strongly cuticularised exodermis. ×405 diam. Treated with hydrofluoric acid.

CONIFERS DAMAGED BY SQUIRRELS.

By Arthur W. Hill

(Assistant Director of the Royal Botanic Gardens, Kew).

[With Plate VII].

THE damage which may be done to trees by squirrels is well shown by some interesting specimens of *Thuya plicata*, D. Don, and *Cupressus Lawsoniana*, A. Murr., sent to the Royal Botanic Gardens, Kew, by Mr. R. B. Rogers of Hexworthy, Launceston, Cornwall, for the Museum of British Forestry.

The specimen of the *Thuya*, a photograph of which is reproduced in the accompanying Plate VII, came from a plantation at Treburtle, near Launceston, where the *Cupressus* was also growing. A large number of these trees have been placed in a mixed plantation of oak, beech, hornbeam, larch and Scots pine during the last twenty years, but the squirrels have attacked only the *Thuya* and *Cupressus*. The injured trees are from 12 to 14 feet high, and the damage was done at least two years ago according to Mr. Rogers' account, which is fully confirmed by the condition of the specimens presented to Kew.

The piece of *Thuya* stem shown in the photograph is four feet high, the diameter of the wood at the base being 1¾-inches and at the apex about 1-inch. There are five islands of cortex and phloem separated completely from one another; in some cases these islands encircle the stem, in others they are unilateral patches. The rings of bare wood separating these islands vary in in width, the lowest seen being about four inches, while the one above is seven inches wide.

The three lower islands were all bearing living shoots when the specimens reached Kew, and in the case of the large island near the base these shoots were about four feet long and quite vigorous.

The islands were consideraby enlarged towards the base, owing no doubt to the accumulation of metabolised products, as is the case in a tree which has been constricted with a tight band. Callus had been formed all round the injured surfaces and at the lower ends of the islands it was as much as an inch in thickness, in contrast to a thickness of only about a ¼-inch on the upper side.

The *Cupressus* is in some ways a more striking example as the islands of the cortex are much more numerous and quite small. In every case a branch forms the nucleus of an island, and some of the islands are so small that callus has not been formed, and the branch has died shortly after the injury. Where larger islands have been left by the squirrels, callus formation, as in the *Thuya*, has taken place, and a conspicuous mass of swollen tissue has developed on the lower portion of these isolated pieces of cortex and bast. The apical portion of the *Cupressus* had died from the effects of the ringing, but the lower branches springing from the healed islands were growing vigorously.

Both the *Thuya* and the *Cupressus* are of about the same age, and judging from the development of callus, the detached islands must have been in a living condition for two or more years.

These cases are remarkable both as an example of the conduction of water in wood unprotected by cortex and bark, and also of the continued conduction of water in old tracheids, since no new xylem can have been added to the now bare patches for at least two years.

No doubt a considerable amount of water was lost in evaporation from the unprotected areas, and in the case of both the trees, the water supply does not appear to have been sufficient to reach to the summit. With regard to the descending current of metabolised products it seems clear from the enlarged condition of the phloem and cortical tissues on the lower sides of the islands that only a small quantity, if any, of the products elaborated by the branches could have been conveyed away to feed the roots. It is possible, however, that a certain amount of sugars may have been carried by a descending current through the xylem of the trunk, as has been shown to be the case in the birches, sugar-maple, etc.[1]

Whether the xylem in the conifers affords a channel for the conduction of sugars, etc. in normal cases, does not appear to have been determined.

The peculiar conditions of life of these living islands on the ringed wooden poles of the trees, suggests a comparison with a partial parasite, such as *Viscum*. These islands, like the parasitic Misletoe plant, are dependent on the tree trunk for their water supply, but otherwise they are independent, since they are able to elaborate and use their own metabolised products. That the existence of branches under such conditions is possible, or rather that the trunk is able to supply them with water, is somewhat contrary to expectation, and it would be a matter of interest to determine for how long a time the water current would be maintained in a completely ringed stem to support life in isolated portions of the cortex.

[1] see Pfeffer. "Physiology of Plants." Eng. Ed., Vol. I, pp. 262, 574, 578, where the author discusses the question of translocation in the wood.

A NOTE ON THE GAMETOPHYTES OF *DACRYDIUM.*

[With Four Figures in the Text].

I. Introduction.

ALTHOUGH we now have a fairly wide knowledge of the early stages of development of the male gametophyte of the Podocarpeæ,[1] yet as regards the female gametophyte and the later stages of development of the male gametophyte our knowledge at present is limited to the observations of Coker[2] on a single species of *Podocarpus* and those of Miss Young[3] on a species of *Phyllocladus*.

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[1] Thibout (1896), Coker (1902), Jeffrey and Chrysler (1907), Young (1907), Burlingame (1908), Norén (1908), Thomson (1909[1]), Brooks and Stiles (1910), Young (1910).

[2] Coker, *op. cit.*

[3] Young *op. cit.*

On the structure of the female gametophyte of the remaining genera we have no information beyond a few isolated facts concerning the megaspore-membrane.[1] This absence of knowledge may serve as an excuse for the publication of the following very fragmentary observations on the gametophytes of *Dacrydium.*

II. MATERIAL.

The material described in this note was kindly sent from New Zealand by Mr. Phillips Turner to Professor Seward, to whom I am indebted for the opportunity of examining it. The material contained ovules of *D. laxifolium*, in which the gametophyte was in a very young stage, and ovules of *D. Colensoi* which had reached a stage just prior to fertilisation.

III. MALE GAMETOPHYTE.

The younger stages of the male gametophyte of several species of *Dacrydium* have been examined by Miss Young.[2] As in all the Podocarpeæ a complex of prothallial cells is produced, which in this genus consists ultimately of three or four cells. The generative cell divides anticlinally into "stalk-cell" and body-cell. The prothallial cells and the stalk-cell come to lie in the general cytoplasm of the pollen-grain and ultimately pass out into the pollen-tube with the tube-nucleus. The body-cell remains behind in the pollen-grain for some time.

The mature pollen-tubes in *D. Colensoi* are large structures relatively to the size of the nucellus, although actually small in comparison with those of some species of *Podocarpus.* In some cases the pollen-tubes branch after penetrating the nucellus.

In *Podocarpus*[3] and *Phyllocladus*[4] the body-cell nucleus produces two unequal male nuclei, and in the latter genus Miss Young was able to shew that two definite male-cells are formed. In *Dacrydium Colensoi* also the division of the body-cell nucleus results in two unequal male nuclei, one of which is non-functional, while the larger functional nucleus takes up a central position in the body-cell cytoplasm (Fig. 4). Owing to the condition of the material examined it was not possible to determine whether definite cells were formed or not.

IV. FEMALE GAMETOPHYTE.

The young female gametophyte in *Dacrydium laxifolium* is found deep down at the base of the long nucellus at about the level where nucellus and integument become free from one another

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[1] Thomson (1905), Norén (1908), Thomson (1909²).

[2] Young (1907). [3] Coker (1902). [4] Young (1910).

(Fig. 1). Its position is thus similar to that of *Phyllocladus*.[1] No intermediate stages have been observed between the young stage of *D. laxifolium* and that of *D. Colensoi* in which the archegonia were ready for fertilisation. The following account refers to *D. Colensoi*.

The number of archegonia varies in the cases observed from one to three, two being very common, and in respect of this small number *D. Colensoi* resembles *Phyllocladus*,[2] but is in marked contrast to the species of *Podocarpus* so far examined, for as the writer is shewing elsewhere, there may be as many as nineteen archegonia in *P. nagi*. The archegonia at the late stage examined appear to be embedded in the prothallus near its apical end (Fig. 2), but this appearance is probably due to a similar sequence of events to that which obtains in *Phyllocladus*. In that genus Miss Young describes the young archegonia as superficial, but when the pollen-tubes come in contact with their necks the adjacent tissues grow rapidly and so leave the archegonia at the bottom of cavities occupied by the pollen-tubes.[3] This same process would account for the condition of affairs seen in *D. Colensoi*. It would also appear that here, as in *Cephalotaxus*[4], the archegonia may become completely enclosed by prothallus tissue if pollen-tubes do not reach their necks (Fig. 3).

The peculiarity of neck development described by Miss Young in *Phyllocladus* and unrecorded for any other genus, also occurs in *D. Colensoi*. This characteristic consists in the separation of the four neck cells from the surrounding cells of the gametophyte, so that they appear as small detached cells against the middle of the outer wall of the archegonium. As in *Phyllocladus* they are,

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[1] Young (1910), Pl. IV., fig. 21.

[2] Op. cit., p. 85.

[3] Young (1910), p. 86.

[4] Coker, W. C. "Fertilisation and Embryogeny in *Cephalotaxus Fortunei*." Bot. Gazette, Vol. XLIII., p. 1, 1907.

Fig. 1. *Dacrydium laxifolium*. Outline drawing of the ovulate structure, shewing the position of the young gametophyte. × 17. *s*, megasporophyll; *e.*, epimatium; *i*, integment; *n*, nucellus; *g*, gametophyte; *b*, sterile bract.

Fig. 2. *D. Colensoi*. Outline drawing of nucellus and prothallus to shew the position of the archegonia. × 17.

Fig. 3. *D. Colensoi*. Outline drawing of the upper part of the nucellus and female prothallus shewing one archegonium with a pollen-tube, and a second one without. The latter is surrounded by gametophytic tissue. × 57.

Fig. 4. *D. Colensoi*. Drawing shewing the male nuclei and the upper part of an archegonium with neck cells. × 267. $♂_1$, functional male nucleus; $♂_2$, non-functional male nucleus; *p*, prothallial (?) nucleus; *n*, neck of the archegonium.

however, connected with the surrounding jacket cells by a membrane (Fig. 4). This condition is due to lateral stretching of the neck and jacket cells owing to the growth of the gametophytic tissues

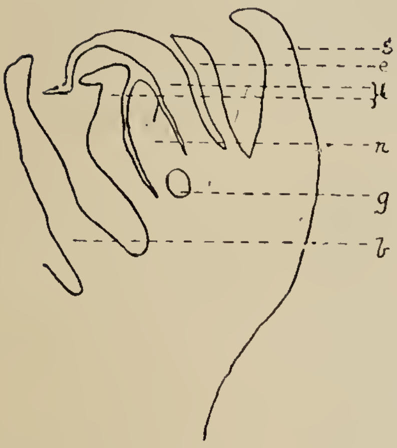

Fig. 1.

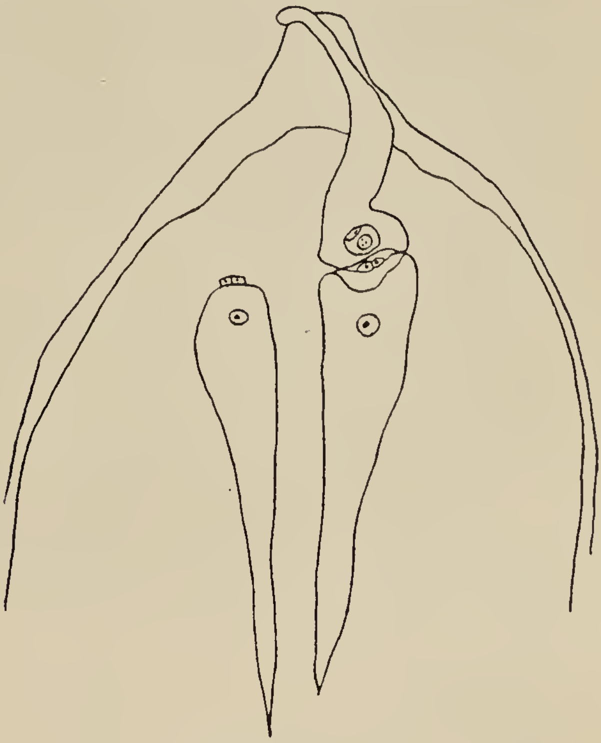

Fig. 3.

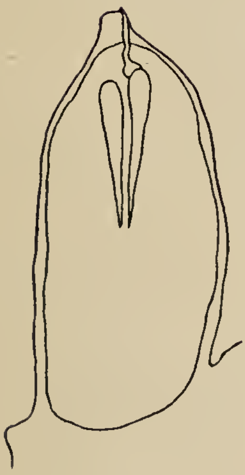

Fig. 2.

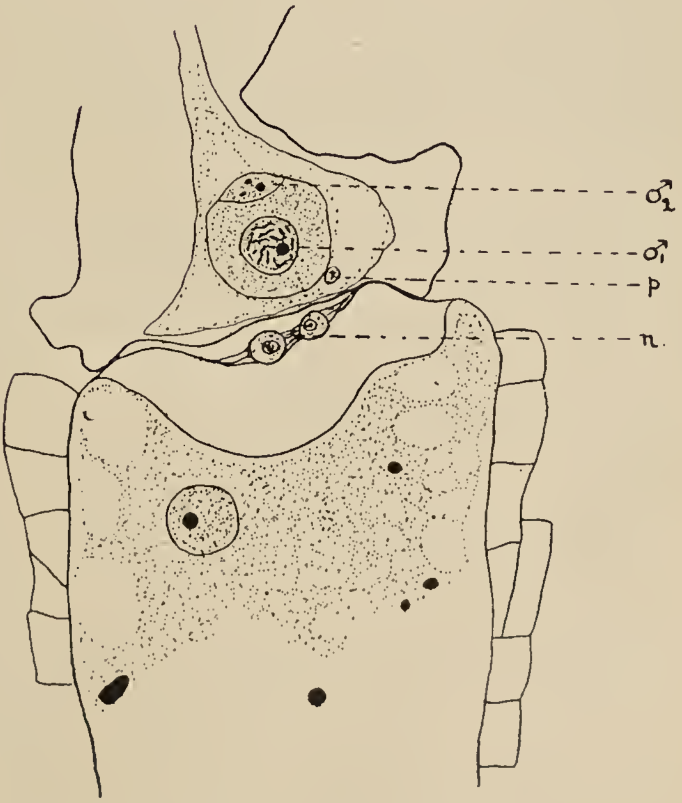

Fig. 4.

For description see p. 344

and the pressure of the pollen-tube.[1] It does not occur in archegonia which have not been reached by a pollen-tube.

The archegonia of *D. Colensoi* are each surrounded by a layer of jacket cells. The shape of the mature archegonium is worthy of notice owing to its extreme length, for it extends to the middle region of the prothallus. It is shaped roughly like an elongated cone, the widest part being that in connection with the pollen-tube; the lower end is very narrow. In the event of a pollen-tube not reaching the archegonium, the upper end is however rounded and narrower.

The cells of the prothallus have by this time become bi- or tri- (and in some cases quadri-) nucleate : a multinucleate condition is also recorded in *Podocarpus* and *Phyllocladus*.

V. GENERAL REMARKS.

These observations on the gametophytes of *Dacrydium*, fragmentary as they are, yet suffice to indicate two interesting facts. The first is the general resemblance of the male gametophyte of *Dacrydium* to this structure in *Podocarpus* and *Phyllocladus*, the second is the much closer resemblance of the female gametophytes of *Dacrydium* and *Phyllocladus* to one another, than to that of *Podocarpus*. This is all the more remarkable as on general grounds the genus *Dacrydium* has generally been regarded as much more closely allied to *Podocarpus* than to *Phyllocladus*; indeed the latter genus has by many writers been placed in a separate order or sub-order, along with *Taxus*, *Cephalotaxus* and *Torreya*. Mr. Brooks and the writer have previously pointed out that the resemblance of *Phyllocladus* to the Taxeæ is not at all striking, while Miss Young has brought forward important evidence in favour of including *Phyllocladus* with the Podocarpeæ. The structure of the gametophytes of *Dacrydium Colensoi* affords a striking piece of evidence in support of this opinion.

THE UNIVERSITY,
LEEDS.
October 20th, 1911.

WALTER STILES.

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[1] Young (1910), p. 86.

LITERATURE.

DEALING WITH THE GAMETOPHYTES OF THE PODOCARPEÆ.

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,, "The Megasporophyll of *Saxegothæa* and *Microcahrys*." Bot. Gazette, Vol. XLVII., p. 345, 1909.[2]

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,, "The Morphology of the Podocarpineæ." Bot. Gazette, Vol. L., p. 81, 1910.

NOTE ON *PELLIA EPIPHYLLA*,

BY T. E. WALLIS, B.Sc, (Lond.), F.I.C.,

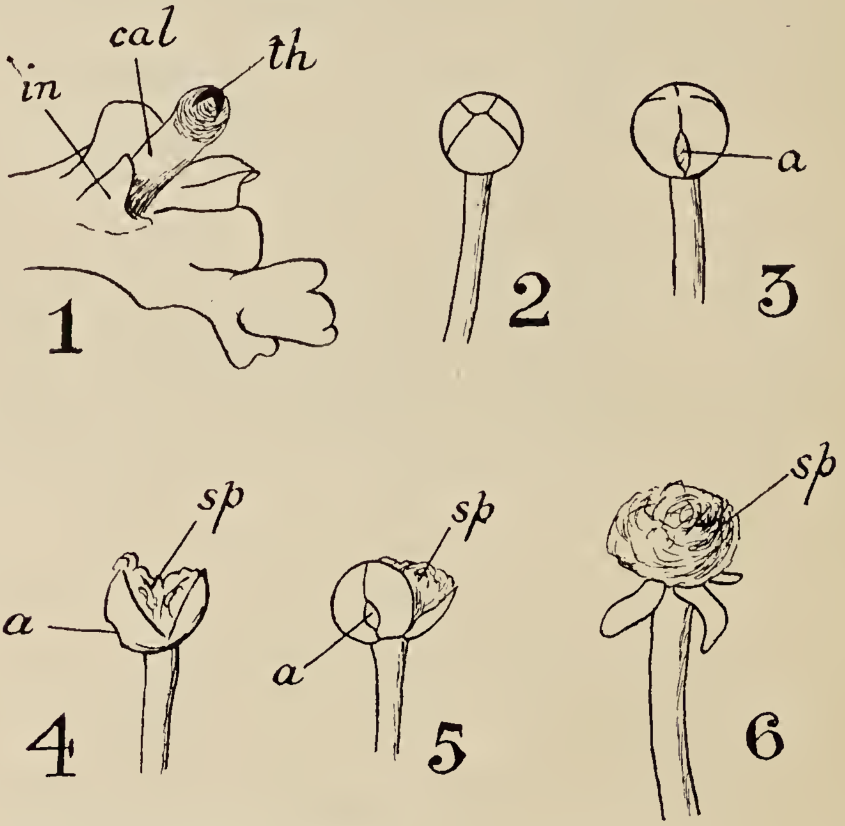
(Lecturer in Botany at the Technical Institute,

Tunbridge Wells).

[WITH SIX TEXT FIGURES].

IT is a pleasure to find in Dr. Cavers' new "Practical Botany" (Clive, 1911) a more adequate treatment of the life history and structure of *Pellia epiphylla* than has hitherto been available; one may instance in particular the description of the dehiscence lines in the capsule wall and the figures showing their microscopical structure (pp. 324 and 326).

Having noticed the meagreness of the accounts usually given, I kept plants of *Pellia* under observation in the laboratory from September, 1910 to July, 1911. As a result I discovered the lines of dehiscence in the capsule wall, and was somewhat surprised to find no mention of them in the ordinary text-books. On looking up the literature relating to the subject, I had found that although the mechanism of dehiscence is discussed in a paper entitled "Grundzüge der Öffnungsmechanik von Blütenstaub und einigen Sporenbehältern," by C. Steinbrinck (Botanish Jaarboek Dodonaea, 1895–6, p. 334), no mention is there made of the special dehiscence lines and it was my intention to publish a small note on the subject: in that, however, Dr. Cavers has forestalled me. There are still one or two small additional facts that I have noted and which seem to be worth recording. The colour of the capsule when it first emerges from the calyptra is nearly black—actually very dark green—and the dehiscence lines are not visible to the naked eye; as the stalk elongates, the capsule turns brown and the four longiduinal dehiscence lines become clearly marked. Dehiscence then takes place, in a curious way; it commences equatorially in two only of the lines, and the splits gradually extend to the poles till the capsule opens in two hemispherical portions; a split then begins to appear in the middle of the back of each these hemispheres along the other dehiscence lines, eventually dividing each hemisphere into two longitudinally, and so forming the four capsule valves. The accompanying sketches, made in March, 1911, will make clear the order of events in the process of dehiscence.



1, Capsule emerging from the calyptra; 2, Capsule turned brown and showing the dehiscence lines; 3, Commencement of dehiscence; 4, Capsule divided into two portions, one shewing the beginning of the second split; 5, Another view of the capsule shown in Fig. 4; 6, Capsule completely dehisced. *in.*, involucre; *cal.*, calyptra; *th*, capsule; *a*, commencement of dehiscence; *sp.*, mass of spores and elaters.

REVIEW.

THE CHICAGO UNIVERSITY TEXT-BOOK.

A TEXT-BOOK OF BOTANY FOR COLLEGES AND UNIVERSITIES by members of the botanical staff of the University of Chicago: JOHN MERLE COULTER, Ph.D., Professor of Plant Morphology, CHARLES REID BARNES, Ph.D., late Professor of Plant Physiology, HENRY CHANDLER COWLES, Ph.D., Assistant Professor of Plant Ecology. Vol. I, MORPHOLOGY AND PHYSIOLOGY. American Book Company, New York, Cincinnati, Chicago, 1910. Pp. viii and 484, and A to L (Index), with 699 figures in the text.

ENGLISH-SPEAKING botanists will turn with considerable interest to the work under review. Elementary text-books of botany are very numerous, but really satisfactory ones which can be whole-heartedly recommended to students, and especially text-books which show real constructive originality are naturally rare. The University of Chicago has deservedly attained a high place among the botanical schools of the world, and its productions of all kinds command attention and respect. The methods of teaching adopted differ in many important respects from those usual in this country,[1] and the whole "atmosphere" is also necessarily somewhat different, so that a book which reproduces in epitome the characteristics of the school cannot fail to interest and instruct British botanists.

The text-book is divided into three parts, Morphology, Physiology, and Ecology, the reponsibility for each being taken by Professor Coulter, Professor Barnes and Professor Cowles respectively. Of these the present volume contains the first two parts, Morphology and Physiology, while the part on Ecology is promised for the present year (1911).

The authors explain their objects in an excellently clear and business-like preface, from which we cite some sentences.

"The three parts of the book . . . . are felt to be the fundamental divisions which should underlie the work of most subdivisions of botanical investigation . . . . We recognize that the presentation of the three great subjects here included is very compact . . . . the student is expected to use it in relating his observations to one another and to the general points of view that the book seeks to develop. There is a continuity of presentation in each part, so that random selection may miss the largest meaning."

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[1] cf. Miss Prankerd's "Botany at Chicago University: some impressions." NEW PHYTOLOGIST, Vol. VII, p. 260, 1908.

"It is important to call attention to the fact that the book has been prepared for the use of undergraduate students. It does not represent our conception of graduate work." [This explains the absence of any citation of literature]. "Still less has this book been written for our professional colleagues, who will notice what they may regard as glaring omissions. Such omissions must be taken to express a deliberate judgment as to what may be omitted with the least damage to the undergraduate student. The motive is to develop certain general conceptions that are felt to be fundamental, rather than to present an encyclopedic collection of facts. This purpose has demanded occasionally also a greater apparent rigidity of form in general statement than is absolutely consistent with all the facts; but it was a choice between a clear and important conception for one with no perspective and a contradiction of large truths by isolated facts, resulting in confusion."

The section on Morphology is strictly evolutionary in treatment. It has nothing by way of preface to the study of Morphology, but begins at once with the Myxomycetes, and considers the groups of the plant-kingdom up to the Angiosperms, so far as possible in phylogenetic sequence. The style is characterised by an extreme lucidity and conciseness which it is difficult to over-praise. There are extremely few ambiguous or obscure sentences in the entire section. The treatment is necessarily highly condensed, and this condensation accounts for an impression of "hardness" that the reader sometimes receives, but the rigorous selection of material which has been carried out has been effected with such care, and for the most part with so nice a judgment, as to leave the impartial critic little reason indeed to justify the authors' fear that "glaring omissions" may be noticed by their professional colleagues. Description and consideration are alike of a very high order of merit. At the end of the treatment of each larger group of plants "Conclusions" summarise the characters of the group and relate it to others, so that the mind is naturally carried along the various lines of descent which are indicated.

This part of the book contains no less than 618 text-figures in 282 pages. They are very largely original, and so far as we have seen, without exception well chosen, extremely clear and excellently reproduced.

The short chapter on Organic Evolution at the close of the section on Morphology is perhaps less satisfactory. There is no fault to be found with its actual statements, which maintain the high standard of the rest of the section, but it leaves the impression that it is of little use to deal with so vast a subject in so short a space.

The following passages in Part I appear to call for comment and criticism.

On p. 16 it is said that "The origin of gametes is the origin of sex, and isogamy is the simplest form of sexuality." This unqualified identification of the sexual process with the process of conjugation, without regard to the binary differentiation inseparably connected with the idea of sex in ordinary language and thought, may no doubt be defended, but it is at least necessary to point out the existence of the decreased connotation of the term as thus used. Otherwise confusion is inevitably created in the mind of the student. The result of reading part of the connotation of sex, as this word is understood in common language, into the process of isogamy, has left its mark on the history of the subject. It is unnecessary to insist on the danger of using common words with altered connotations in technical senses.

In describing *Pandorina* (p. 17) the opportunity is missed of illustrating the origin of sex in the common sense, *i.e.*, the binary differentiation of gametes. The life-history of *Pandorina* as described by Pringsheim is of fundamental importance precisely because it illustrates this phenomenon. The evolution of a *soma* in *Pleodorina* and its increase in size and importance in *Volvox* is not brought out, all reference to the former genus being omitted. The evolution of the Volvocine series is one of the most instructive of all evolutionary stories, since it illustrates far better than any other the most fundamental differentiations in the organic world.

The use of the word "irregular" as applied to chloroplasts of Desmids (p. 37) tends to convey a misleading impression.

In dealing with *Chara* it is said, on p. 42, that "The axillary position of the main branch suggested that the smaller subtending branches are leaves." This statement appears to require elaboration to make its significance clear.

It seems a mistake to base the discussion of alternation of generations in the algæ (pp. 31, 51, 60) entirely on the "chromosome test." Such a limitation must give the student a rigid and one-sided idea of a difficult and complex subject.

The dominance, in America, of the pure antithetic theory of alternation as elaborated by Bower is reflected in the accounts of *Anthoceros* and of the Lycopodiales. These accounts, with the theoretical paragraphs attached to them, carefully stated and qualified as they are, deliberately put before the student one view only of this highly debateable topic. This is no doubt an expression of the "deliberate judgment" referred to in the preface, but it is permissible to doubt the soundness of that judgment in this instance, considering the present state of knowledge and opinion.

It is said on p. 121 that "the central region of the stem and seta of Polytrichaceæ almost suggest conducting tissue." On page 342, in the physiological part of the book, the experimental evidence for conduction in the central strands of elongated cells of "the sporophytes of liverworts and mosses" is said to be "weak." This last statement is to some extent true, but it is difficult to understand how anyone acquainted with the structure of the Polytrichaceous stem can doubt the conducting functions of the comparatively highly differentiated central cylinder. The words "almost suggest" convey quite a wrong impression of the facts.

On page 143 it is stated that the partition of the synangium of *Tmesipteris* is sterilized sporogenous tissue, and that this is "proved by its development and by the fact that in exceptional cases it functions as sporogenous tissue;" also that in *Sphenophyllum* the "sporangiophore development is carried much farther than in *Psilotum* and *Tmesipteris*, resulting in a multiplication of sporangia by means of the sporangiophore." The evolutionary theory here suggested is a possible one, but it is not the only possible one, and no part of the evidence for it can be fairly described as "proved" by any known fact.

The description and figure (140) of the vascular bundles of *Equisetum* are not at all good. The xylem is said to be "hardly at all developed, its position being occupied by a small air passage (p. 146)." Not only the primitive protoxylem strand of the internode, but also the lateral metaxylem strands and the nodal xylem are thus quite ignored.

The word *polystele* is used (on p. 157) in the sense apparently of *polydesmic stele*, for it is said to be the condition "in which several concentric bundles traverse the stele without organisation into a definite cylinder." Both the word and the definition are open to objection—the word because it suggests the well-known word *polystelic* which means "having many steles," and the definition because the emphasis should be laid on the fact that a cylinder is still present, but is perforated by gaps. The stele of *Pteris aquilina* is not, like the cauline vascular system of certain astelic angiosperms "without organisation into a definite cylinder," but is perforated by gaps having a considerable, but not an unlimited, variability in size and position.

It is scarcely correct to say that "all of the four kinds of bundle (? stele) described above as occurring among ferns are prevailingly mesarch." In a very large number of cases, probably the majority, the steles of ferns are endarch, *i.e.*, the protoxylems are developed on the inner limit of the xylem.

The paragraph about the relation of apogamy and apospory to the number of chromosomes (p. 170) should, we think, have been elaborated. Some indication of the fact that apospory and apogamy are often associated in the same life-history, and of what happens to the number of chromosomes in such cases, is surely required.

It seems a mistake to illustrate the structure of the apical meristem of angiosperms by a figure of *Hippuris*, which has been shown to represent a rare condition of the layered meristem.

The term "dotted ducts" (p. 241) is surely an obsolete and unnecessary synonym for pitted vessels; and why should the *tracheids* of pteridophytes be "known as scalariform *vessels*"?

On p. 243 it is said that the vascular system of the mature stem of dicotyledons "consists of a hollow cylinder composed of vascular bundles and inclosing the pith (a siphonostele). Traversing the vascular cylinder from the pith to the cortex, and hence separating the bundles, are the pith rays." The second sentence ignores the pericycle, and regards the bundles of a typical dicotyledon as isolated strands running through ground tissue, separated topographically into cortex, pith and "pith rays." This position, if it is really intended, seems to take us back to the days before the doctrine of the stele was established. The term "pith-ray" or "medullary ray" has become rather misleading as applied to the rays of the typical dicotyledon. If, however, the position be defended, it is inconsistent with calling the vascular system a "siphonostele," especially when we consider the description of the the vascular system of *Pteris* on p. 157 as already criticised.

Surely it is an exaggeration to say (p. 245) that the amphivasal bundle is "characteristic" of the mature stems of monocotyledons.

The description of secondary thickening of the vascular cylinder of a root (p. 248) is not quite satisfactory, nor does it quite tally with Figs. 556 and 557. There can be no "primary pith rays" in a root of the primary structure represented in Fig. 556, which has no pith at all, but a solid tetrarch primary xylem star. Neither can such a root (nor indeed strictly speaking any root) "lose any appearance of its primitive radiate structure." It is only its secondary tissues which can "assume the appearance" of those of a dicotyledonous stem.

On p. 265 the three cells of the egg-apparatus are described as "all potential eggs." On p. 275 it is said that "the synergids . . . have been observed to produce embryos, and since these cells are gametophytic, these embryos arise by vegetative apogamy (see p. 169)." On p. 169 vegetative apogamy is defined as the case of an embryo arising "from the vegetative tissue of the prothallium." Is this implied inclusion of the synergids with the vegetative tissue of the prothallium intended?

On p. 278 it is said that the Liliales show "a distinct development from hypogyny, as in the amaryllises (Amaryllidaceæ) to epigyny as in the flags (Iridaceæ)." For "amaryllises" we should presumably read "lilies."

Many of the foregoing criticisms are, of course, criticisms of detail and in some cases of the form of expression, but the book sets so high a standard of lucidity and exactness of statement that we feel sure the authors will expect an equally rigorous standard of criticism. An attempt has been made to limit criticism according to the ideals and principles which have guided the authors as set forth in the preface; but in writing detailed comment of this kind on such a book it is impossible to convey to the reader a just idea of the overwhelming preponderance of exposition which seems beyond criticism.

Part I of the book is, in the opinion of the reviewer, by far the best elementary account of the "special morphology" of the plant kingdom, given the limitations deliberately adopted, that has yet appeared. A. G. T.

THE remainder of this volume deals with the Physiology of Plants and was written by the late Professor Barnes. The writer to whom the reviewer's pen is now transferred would wish that something of the serene appreciative power of his colleague might still remain in that pen; but of physiology it can still be said, to the sorrow of the teacher and the joy of the investigator, that many comparatively superficial phenomena are as yet quite uncomprehended, and in touch with this ignorance the hand of criticism falters.

Some added unsteadiness comes too from the knowledge that the author of the second part of the Chicago Text-book will teach no more and that the Botanical Gazette will lack those model "Notes for Students" on physiological topics which delighted us by their frank criticism and brisk judicial evaluation.

As in those notes so in this book, one sees Barnes as a teacher rather than a worker. He feels strongly the duty of selecting for his audience and he does his duty wlth gladness, so that this last writing bears a deep impress of his personality.

Perhaps the most interesting treatment for this notice will be to select for comment some of the special personal characteristics of the author's outlook on the physiology of plants.

After an introductory page which is designed to lead over from morphology to physiology we come to two chapters entitled respectively "The Material Income of Plants" and "The Material Outgo of Plants." These contain a curious selection of topics, as both respiration and assimilation are excluded from them. The intake and the output of water are the main topics and one wonders whether putting these in the forefront of physiology—to the degrading of the more fundamental vital functions—is due to the fact that for the first time in an important text-book the subject of ecology takes rank on an equal footing with the older divisions of morphology and physiology: for the ecological forms of plants are, of course, correlated more closely with water-questions than with "protoplasmic" functions.

Barnes' personality comes out at once in his treatment of the relation of the plant to water. He emphasizes the enormous amount of water present in plant-tissues and says that were this only *visible* everyone would recognize that "a plant may justly be spoken of as water, held in form by other substances mingled with it." He admits that this is quite the reverse of the ordinary conception and indeed we have only to turn to the Bonn Text-book, to a corresponding point in Noll's exposition of the water-relations of the plant, to read "Plants, in spite of the great amount of water contained in them, are of the nature of solid bodies" (3rd English Ed., p. 173).

It is a nice question for philosophical discussion to determine which is the more important point of view to insist on—the continuity of water through the whole plant, cell-wall, protoplasm, sap-vacuole—or the discontinuity of properties between these three parts. While both aspects have very great importance the reviewer cannot help feeling that if selection must be made, the place of honour should be allotted to the colloidal organisation of protoplasm, whereby a stable vital machinery is built up on a basis of some 5% of solid matter and 95% of water. It is rather surprising to note that the word "colloid" nowhere occurs in this physiology.

Another aspect of the relation of the plant to water, on which Barnes is strongly partisan, is the question of the significance of transpiration. Is it of profound biological advantage and the plant-structure adapted to promote it, or is it a necessary evil of the environment in which land plants grow—the last infirmity of noblest vegetation? To the best of the reviewer's knowledge, though various distinguished workers have held the latter view, this is the only text-book that puts aside resolutely the evidence for the former, and is content to teach its students only the latter in its entirety. On p. 326 we read "Transpiration, far from being a function of plants, is an unavoidable danger." This view is elaborated at some length and is in striking contrast with the statement in the Bonn Text-book, mostly read by our undergraduates, where we read "Were transpiration not in the highest degree useful and even necessary for the acquisition of mineral substances, provision would certainly have been made by plants to restrict it within the narrowest possible limits" (p. 197).

It is not easy to argue wisely about what is or is not, on the whole, an advantage to the plant. What we really lack is critical experimentation on the growth of ordinary mesophytes when transpiration is reduced nearly to zero. This only requires experiment on a properly large and expensive scale, and what one would have admired most in an American text-book would have been a statement that we are ignorant on this fundamental point and an appeal that $5,000 spent on special constructions would certainly provide the answer.

The reason that Barnes gives for the faith that is in him is that "it is *impossible to reconcile with present ideas* of osmotic movement" the conception of a transpiration current sweeping in needful mineral salts from outside the roots. Pure water he admits it may sweep in, to replace water lost in leaf-evaporation, but the dilute salts outside cannot be drawn in through the root-cortex against the stronger concentration of salts within the plant. We see that the bases of his objections are not so much definite experiments as human ignorance (note the words we have italicised).

A connecting factor undervalued by those who hold with

Barnes that intake of water at the root-surface and intake of salts in solution are quite separate processes is that this very intake of water must concentrate the solution on the surface of a root growing in soil till its salt-concentration possibly exceeds that of the root cortex and a diffusion-gradient in the right direction is established. Apart from such considerations our knowledge of protoplasmic permeability, its variations and mechanism, is now advancing rapidly and we see that ignorance is not a safe ground to build on. It is quite possible that the "translocation" of salts is really some special process not yet understood and as effective upwards as the downward translocation of organic substances in the phloem, which is carried on without an actual mass-current.

Barnes admits that transpiration is "a possible advantage" in one way (p. 326) by causing a relatively rapid mass movement of solutions in that part of the ascending water-path which is not concerned with protoplasm and osmotic phenomena. Since in a tree fifty feet high the path of a water-molecule in the transpiration current lies for only a few millimetres among living cells (in root-cortex and in mesophyll) and for ten thousand times that distance among dead conduits, it follows that any advantage due to transpiration in this major portion of the route must bulk largely in the total summing-up.

It is unexpected to find in the treatment of exudation of water no echo of Lepeschkin's classical paper of 1906 which expounded so clearly the mechanism of exudation in the sporangiophore of *Pilobolus.*

Chapter III deals with nutrition and opens at once with a characteristic long discussion of the exact sense in which one should use the word "food" in connection with green plants. Is it legitimate to speak of carbon-dioxide and salts as the food of green plants and say these plants live on inorganic food, or must we say that these ingesta are only *raw materials* and that from them the plant makes its own food? Obviously the full conception of "food," so clearly understood in relation to animals, does not apply to plants, and there are difficulties in any use of the word. Yet we think the student with a physical training will revolt more against the idea of any organism making its own food, as contrary to the "conservation" of something or other; and rightly indeed, for from the point of view of energy the plant does not make its own food, but the energy descends upon it from above, like manna in the wilderness.

Such a discussion is of course not useless, but the author's temperament leads him to give full play to it, rather than to state the facts of plant-nutrition as an independent series of consecutive phenomena and leave the student to try for himself which is the least unsatisfactory misfit of the alien word "food."

A little further on the expression "*carbon-assimilation*" comes in for a not altogether unmerited share of contempt; yet some delay in the universal substitution of "*photo-synthesis*" is justified until we know that light really takes part in the synthesis as well as in the photolysis.

There are several careless statements in the sections dealing with the intake of carbon-dioxide. On p. 365 it is said that water-plants are "in a very advantageous position as far as a supply of CO_2 is concerned because of the great solubility of that gas in water," but the sluggishness of gas-diffusion in water more than counterbalances this solubility.

A little further on it is stated that CO_2 dissolves so readily in the wet walls of the mesophyll that the pressure of CO_2 in the intercellular passages is usually zero. The evidence is against this, and on Horace Brown's calculation the CO_2-pressure in the air inside the leaf is very little less than that of the air outside.

The chemical statements about chlorophyll and the accompanying plastid-pigments are not at all near to the state of knowledge in 1910, and the author has actually introduced a name of his own for pure "chlorophyll," to wit, *chlorophyllin*, which is already allotted by workers on the subject to a chlorophyll-derivative.

Chapter IV deals with destructive metabolism. The most important of these processes is respiration, to the theory of which, Barnes had given special attention. He is strongly of opinion that all respiration is primarily protoplasmic breakdown, that food material is never oxidised directly in the cell and that the comparison of respiration to any sort of combustion is more misleading than helpful. He certainly exposes very well our uncertainty as to the precise significance of respiration in the cell.

Fermentation is very briefly dealt with and little sympathy is shown with the discovery that alcoholic fermentation can proceed apart from protoplasm.

Chapter V contains the whole of growth and movement, and it is in the latter part of this last chapter that one feels that the very condensed writing is not quite ideal for treating the more subtle difficulties of irritability, though the handling of these is otherwise good.

On the whole this is certainly a well-knit lucid account of the author's conception of the plant as a physiological organisation and though the reviewer cannot agree with several views that are warmly expounded by the author, yet it is pleasant to meet in print this vigorous personality and one regrets very much that it is for the last time. F.F.B.

NOTES ON RECENT LITERATURE.

Recent Researches on *Williamsonia*.

[With Two Figures in the Text].

SINCE the publication in 1870 of Williamson's classic paper on *Zamia* (*Williamsonia*) *gigas*, our knowledge of the Bennettitales has received few additions from the study of the Jurassic Flora of Yorkshire. The materials collected by the earlier workers, Williamson, Bean, and Leckenby had been re-examined and considerable difference of opinion had been expressed with regard to them, but no very definite conclusions had been reached. In view of the rather unsatisfactory state of preservation of the Yorkshire remains this is not surprising, but it has remained for Professor Nathorst of Stockholm not only to contribute very materially to our knowledge of these forms, but also to introduce methods of studying them which are of the greatest value. It had long been recognised that many of the Jurassic fossils were not entirely structureless and that by treating them with nitric acid and potassium chlorate, the form of the cuticular cells, of the stomata and of spores could be made out, but this method had not yielded many important results. Professor Nathorst has improved the process and used it with great success especially in the investigation of microsporangia.

The results of the investigations on the "flowers" of Williamsonia have been published in two papers, the second of which recently appeared. In the first paper[1] he describes his re-investigation of the species previously known (*Williamsonia pecten*, *W. gigas* and Williamson's carpellary disc) together with some important new forms (*W. spectabilis*, *W. Lignieri*). He further describes the flowers of the interesting Swedish *Rhætic* form *Williamsonia* (*Anomozamites*) *angustifolia*, which he now places in a new genus *Wielandiella*. In the second paper[2] the Yorkshire *Williamsonia* "flowers" are treated more critically and several interesting new species found by Dr. T. G. Halle are described.

The "flowers" of *Williamsonia* were probably mostly unisexual: as yet, no certain case of an hermaphrodite structure has been found. In this respect therefore, they probably differ from the American *Bennettites* (*Cycadeoidea*). The male flower consisted of a number of microsporophylls, more or less united into a cup-shaped structure at the base, and either sessile, or as in *W. spectabilis*, borne on a stout stalk. On the free upper parts of the sporophylls sessile reniform synangia are seen, in which the microspores were produced. In

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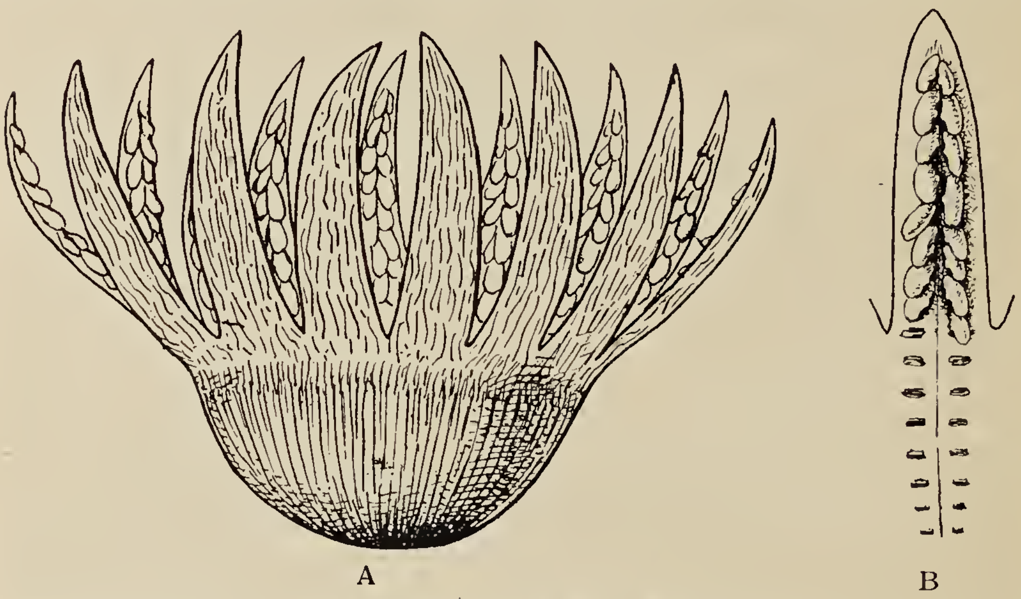
[1] Paläobotanische Mitteilungen, 8, K. Svenska Vet. Akad. Hand., Bd. 45, Nr. 4, 1909.

[2] Paläobotanische Mitteilungen, 9, K. Svenska Vet. Akad. Hand., Bd. 46, Nr. 4, 1911.

general arrangement the synangia are somewhat similar to those of recent Cycads, being, however, on the adaxial or upper side of the sporophyll. The synangia vary considerably in number and arrangement. In *W. spectabilis* they appear to be crowded together irregularly, and it is suggested that the sporophyll may be analogous to a pinnate frond bearing simple pinnæ below and lobed ones nearer the apex. In *W. whitbiensis*, however, the synangia show a much more regular arrangement (cf. figure). They are attached to the sporophyll by their short side and lie in two rows, one on either side of the axis. It is not possible to say whether the synangia were stalked or not, but if stalked the stalk was very short; in the lower part of the calyx (Becher) they were rudimentary. There seems to be little doubt that the much discussed "carpellary disc" of Williamson was a structure somewhat of this nature. The arrangement of synangia in some of these Yorkshire forms is therefore similar to that seen in the *Williamsonia* from Mexico figured by Wieland,[1] where the synangia are borne in two rows on a reduced sporophyll which is fused to the calyx-like united bracts. But in the Yorkshire specimens, no sporophylls distinct from the cup-like bract segments can be distinguished.



Restoration of ♂ flower of *Williamsonia whitbiensis* Nath. Nat. size. (A), Complete example. (B), A single sporophyll showing the form and attachment of the synangia, and the markings below them, which probably represent rudimentary synangia. From fig. by Professor Nathorst. cf. Pal. Mitt., No. 9, p. 13, fig. 3.

The male "flower" of *Williamsonia* thus presents a considerable difference from the microsporophylls of the Bennettitean strobilus, the synangia being borne on the surface of a flattened entire calyx-like structure and not on a highly-divided reduced frond-like structure.

The female strobilus of *Williamsonia* is, however, almost identical with the corresponding structure in the genus *Bennettites.* The ovules are borne on stalks on a swollen receptacle among numerous peltate interseminal scales. The external surface of the mature strobilus is quite characteristic, being divided up into the hexagonal areas of the interseminal scales with the micropylar tubes projecting among them. Two species of female "flowers" differing in general form have been distinguished, one having a spherical, the other a pyramidal external shape. By treatment with acid the form of the cells of the interseminal scales and the micropylar tubes are clearly seen. It is not known whether the flowers of all the Williamsonias were surrounded with a perianth-like ring of bracts; in the original *W. gigas* this was doubtless the case, and in the beds containing the other strobili numerous separate bract-like structures of doubtful affinity are found, but no specimen is yet known which has such bracts in place.

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[1] Wieland. The *Williamsonias* of the Mixteca alta., Bot. Gaz., p. 427, 1909.

Professor Nathorst's work and my own observations lead to the conclusion that plants allied to *Williamsonia* formed a considerable part of the Lower Oolitic Flora of Yorkshire. It is probable that most of the Jurassic Cycad-like fronds should really be associated with these plants, though at present the only evidence of actual connection is found in the case of *Wielandiella* (*Anomozamites*). Professor Nathorst holds the view, however, that it is at present wise to retain the old form-generic names for the leaves where actual connection has not been proved. He therefore rejects the use of the term *Williamsonia* as applied to the fronds usually known by that name, and retains the original designations of *Ptilophyllum* and *Zamites* for them.

One of the most interesting results which this work has furnished. concerns the number and arrangement of the microsynangia. While in *W. spectabilis* these are very numerous and rather irregularly scattered over the sporophyll, yet they are apparently not so plentifully produced as in *Bennettites*. In *W. whitbiensis*, however, the number is very considerably reduced. The lower ones are sterile, and in the restoration given, there are about eighteen synangia to each sporophyll. If it is safe to draw any conclusions from Williamson's "carpellary disc" it would appear that the functional sporangia were reduced to two on each sporophyll.[1] In a yet undescribed allied form (*Williamsoniella coronata*) in my collection, there are five or six synangia on each sporophyll, so that the smaller number is not exceptional. The "flowers" of *Wielandiella* also exhibit an advanced stage in the reduction of the microsporangia. Here the latter are few in number, sessile and arranged in the form of a ring or flange round the lower part of the receptacle. They seem to be situated directly on the axis and show no traces of sporophylls. They can therefore be compared somewhat closely with a whorl of sessile stamens, in which the anthers are more or less united. Whether the Bennettitean type of microsporophyll is more primitive and the *Williamsonia whitbiensis* type a derived form, is largely a matter of conjecture, but there seems to be some evidence in favour of such a view. It is, however, clear that the excellent work which Professor Nathorst has done will lead to interesting results.

H. H. T.

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[1] This view is adopted by Schuster, who has recently described *Weltrichia*, another genus of the Bennettitales, and has tried to trace the actual steps in the evolution of the Ranalian flower from the Bennettitalean strobilus. Schuster, K. Sv. Vet, Akad. Hand. Bd. 46, No. 11, 1911.

MEDULLARY RAYS AND THE EVOLUTION OF THE HERBACEOUS HABIT.

1. A. J. Eames: "On the Origin of the Broad Ray in *Quercus*." Bot. Gaz. XLIX., March, 1910.
2. I. W. Bailey: "Reversionary Characters of Traumatic Oak Wood." Bot. Gaz. L., November, 1910.
3. Ibid: "The Relation of the Leaf-trace to the Formation of Compound Rays in the Lower Dicotyledons." Ann. of Bot. XXV., January, 1911.
4. A. J. Eames: "On the Origin of the Herbaceous Type in the Angiosperms." Ann. of Bot. XXV., January, 1911.
5. W. P. Thompson: "On the Origin of the Multiseriate Ray of the Dicotyledons." Ann. of Bot. XXV., October, 1911.
6. Percy Groom: "The Evolution of the Annual Ring and Medullary Rays of *Quercus*." Ann. of Bot. XXV., October, 1911.

THE series of papers whose titles are given above, embody the results of an interesting and important series of researches into the structure and phylogenetic connexions of the different types of medullary ray occurring in dicotyledons, and of the relation of ray-formation to the evolution of the herbaceous habit among Angiosperms. They all (except the last) emanate from the Phanerogamic laboratories of Harvard, where the work was carried out under the general direction of Professor Jeffrey.

The aggregation of a number of closely approximated uniseriate rays in certain longitudinal bands of the secondary xylem occurs in a number of Cupuliferæ, and to these the name "false ray" has sometimes been applied. The occurrence of these "false rays" in the wood of a Miocene Oak led Eames (1) to investigate their relation to the typical broad multiseriate rays of modern oaks. It was found that several tertiary oaks had rays of this kind and that the same condition was demonstrable in the seedlings of several existing black or red oaks (*Erythrobalanus*). In the seedlings of the white oaks (*Lepidobalanus*) the uniseriate type of ray alone exists; while in the later formed wood of these seedlings, as in the earliest wood of "black" oaks and in the twigs of adult "live" (evergreen) oaks, various stages of the "compounding" of these uniseriate rays occur. In this process of fusion of the uniseriate rays, fibres and wood-parenchyma-cells are often included in the compound ray. Eventually we come to the typical broad homogeneous rays of the adult deciduous oaks, which clearly form the term of this series of conditions. It seems difficult to read the series as other than progressive, so that we may conclude that the broad ray of the modern deciduous oaks is a compound structure orginally derived in descent from the fusion of a number of uniseriate rays. Numerous uniseriate rays co-exist, of course, with the compound rays in the wood of the modern oaks.

An interesting confirmation of this conclusion was found by Bailey (2) in wounded oakwood. The secondary wood formed immediately external to the seats of wounding contained only uniseriate rays, but in the later formed wood all stages of the compounding of these to form broad rays were met with. Jeffrey has given good ground for believing that in several instances traumatic areas of tissue show reversionary characters, and the evidence of the wood formed after wounding in oaks thus supports the theory of compounding based on palæontological and ontogenetic evidence.

In a second paper (3) Bailey discusses the cause of the aggregation of ray-tissue along certain radii which is found in the formation of broad as opposed to narrow rays. He extends Eames' results to

Alnus and other Cupuliferæ as well as to various other woody plants, and concludes that it is the influence of the leaf-trace on the secondary wood which brings about the aggregation of ray-parenchyma in the neighbourhood of the point at which the trace enters the cylinder. In the course of its passage through the secondary wood the trace exercises a disturbing effect on the tissues "expressed by a diminution of the number of vessels and by the increase of storage tissue, particularly by the enlargement and multiplication of the rays." In some cases this aggregation of ray-tissue is confined to the immediate vicinity of the leaf-trace; in others (e.g., *Alnus japonica*) it extends upwards, and especially for some distance below the point of exit of the trace, and in transverse section several compound rays may be seen belonging to the traces of several nodes situated at various levels above the plane of section.

In the "live" (evergreen) oak (*Q. virginiana*) a relatively primitive condition obtains, in which there is comparatively little parenchymatous tissue above and below the leaf-trace during the first few years of growth; but later on, as may be seen from tangential sections taken through the younger wood, a long compound ray stretches down below the trace. In transverse sections taken below the trace this ray is seen to begin at some distance from the pith.

In the deciduous oaks broad ray-formation in relation to the leaf-traces has been carried much further. In the "white" oaks these rays are developed mainly in connexion with the lateral bundles of each leaf-trace, and there are generally ten of them to be seen on a transverse section of the secondarily thickened stem, one pair corresponding to each lobe of the primary five-lobed stele. In the mature twigs of the "red" oaks the tendency to form compound rays has become more firmly established and numerous broad rays are formed in the secondary wood in addition to those connected with the lateral leaf-traces.

The explanation of the differences between evergreen and deciduous oaks put forward by Bailey is that the alternation of seasons related to the deciduous habit has necessitated the formation of much more storage-parenchyma than appears in the evergreen forms.

The broad rays are stated by Bailey to exercise a marked retarding effect on the rate of growth in thickness of the stem in the tracts which they occupy, so that the external surface of the wood, as seen when the tree is barked, may show a fluted character, the furrows corresponding with the broad rays. In some cases (e.g., *Carpinus caroliniana*) this fluting extends to the surface of the twig itself. This is an interesting phenomenon, of which no explanation is offered by the author. Can it be due to the difference in the water supply to the cambium opposite the rays, as opposed to that available where tracheids abut on the cambium? One would have supposed that the rate of production of new tissue by the cambium would depend rather on the supply of organic substance. In this connexion it would be of interest to know how far the evolution of the phloem rays follows a parallel course to the rays of the xylem. This subject is not referred to in any of the papers under review.

Simultaneously with Bailey's paper (3) on "The Relation of the Leaf-Trace on the Formation of Compound Rays," there appeared a very interesting paper by Eames (4) on "The Origin of the Herbaceous

Type in the Angiosperms." The author points to the fact that no undoubted herbaceous types of vascular plants are known from the older rocks: to the herbaceous character of the modern representatives of the great arborescent Pteridophytic stocks which flourished during later Palæozoic times: to the arborescent character of practically all Gymnosperms: to the preponderance of herbaceous forms among the derived groups of Angiosperms, *e.g.*, the Monocotyledons and the higher Sympetalæ: and concludes that there is a great deal of evidence tending to show that arboreal forms are relatively primitive and herbaceous forms derived. He then proceeds to enquire as to the factor which has led to the production of the typical anatomical structure of the herbaceous stem from that of the woody plant. He finds this factor in the influence of the leaf-trace. The extension of parenchyma from the neighbourhood of the node in vertical radial bands forming broad rays, as described by Bailey, eventually dissects the woody cylinder into wedges. The cambium at first extends across the broad rays and produces "inter-fascicular tissue," but in a later stage of the progression is restricted to the bundles themselves, and ultimately (as in Monocotyledons) dies out even in them. Certain genera of Rosaceæ with persistent woody underground rhizomes and herbaceous aerial stems were found to be very instructive in this connexion. The more or less woody rhizomes of several species of *Potentilla*, for example, show broad alternating wedges of tracheids and parenchyma. Each parenchymatous band has, however, a small group of xylem on its medullary border, and these groups are found to be leaf-traces. If the wedges of secondary xylem were reduced in size a structure would be arrived at such as is found in many herbaceous forms. At the base of the aerial stems of various species a continuous woody cylinder occurs: as the stem is traced upwards, the leaf-traces are gradually isolated and the ring of bundles that eventually remains is composed of traces and "common" bundles of the stem. Taken together with the fact that the epicotyledonary seedling stem of many herbaceous angiosperms has a continuous ring of primary xylem (as shown in several cases by Professor Jeffrey and others), which breaks up into distinct bundles as it is traced up into the later formed stem, such phenomena as these furnish a very good foundation for the belief that the typical stele of herbaceous plants with separate bundles showing little or no secondary thickening is essentially a derived type whose ancestors possessed a continuous primary xylem ring which underwent secondary thickening.

Both Eames and Bailey point out that such a theory directly contradicts the view which would regard the herbaceous type as primitive, and secondary thickening as arising first in the bundles, and later by means of an "inter-fascicular cambium" extending between them and uniting the originally separate bundles into a woody cylinder. Though the facts have often been stated in such a way as to imply a theory of derivation of the woody from the herbaceous type we doubt whether such a view has been held, as a deliberate phylogenetic theory, at all so widely as these authors believe. Bailey says that this conception originated with Sanio, was "exploited" by Sachs and De Bary, and has been since adopted by subsequent "authoritative writers." It is, perhaps, difficult for the younger workers of the present generation, who have always been used consciously to apply the method of comparison with a view to phylogenetic conclusions, to realise how little such methods were adopted forty, or even thirty, years ago. The phylogenetic standpoint is conspicuously absent from the writings of most of the workers of De Bary's generation, and in the writings of Sanio (so far as the reviewer is aware) there is no expression of any such phylogenetic theory as the one indicated. Nor is there anything in Sachs' "Lehrbuch" (alluded to by Bailey) which implies anything of the kind. Sachs describes the primary structure and secondary thickening in the *hypocotyl* of *Ricinus communis* quite correctly in the main; the mistake he made was in taking it as typical of the structure of the dicotyledonous stem (epicotyl). No doubt many text-books have repeated Sachs' mistake and stated the facts of structure in a misleading and even an inaccurate way, but there has scarcely been in existence a deliberate phylogenetic theory which derived arboreal from herbaceous plants in the way indicated.

Thompson (5) has extended the researches of Eames and Bailey to *Casuarina*, the Ericaceæ, and the Proteaceæ, and concludes that in these woody plants, as well as in various Betulaceæ and Fagaceæ, the broad "compound" ray has, during descent, been broken up to form what he calls "multiseriate rays," two or more cells wide (sometimes also uniseriate rays) which have "spread through the wood in the higher dicotyledonous Angiosperms." "Reversion" to the broad "compound" form is found in the seedlings of some of these forms. The broad compound ray is often found in association with the leaf-trace, and breaks up into several "multiseriate" rays as it is traced outwards and upwards through the secondary wood. In other cases no broad rays are found at all.

This interesting work is being continued in Professor Jeffrey's laboratory in various directions and certainly shows that the comparative study of secondary tissues is likely to give results of phylogenetic significance. But considerable caution is needed in accepting far-reaching conclusions based on rather narrow foundations. When we are told that the broad rays of the oak-type are on the one hand compounded of primitive uniseriate rays, and on the other hand may break up into multiseriate (narrow) and apparently also into uniseriate rays, it is obvious that the greatest care is required in interpreting the results of observations. Particularly the tendency to interpret the changes which occur in the progressive formation of a given ray or group of rays at a given point in the stem in terms of phylogenetic change in the rays of a genus or group of species needs very careful checking. This tendency is rather conspicuously apparent in Thompson's paper (5).

It seems a pity that the illustrations of all these papers (as is generally the case with the anatomical work of Professor Jeffrey and his pupils) should be rigidly confined to photographs of sections. In some cases these photographs show clearly what they are intended to show. In other cases they do not, and should be replaced or supplemented by drawings and diagrams if the structures described are to be made completely clear to the reader.

Professor Groom (6) devotes the second part of his paper to a consideration of the evolution of the medullary rays of *Quercus* as a result of the investigation of the secondary wood of a considerable number of species. He contemplates the possibility of evolution having proceeded in either direction—from broad rays to narrow ones by subdivision, or from narrow rays to broad ones by aggregation—or in both, and refuses to decide between the alternatives.

He criticises the work of Eames and Bailey, justly we think in regard to the interpretation of the replacement of narrow rays by a broad one in successive annual rings. He also says that the facts with regard to the wood of seedlings "lose their significance if it be shown that a similar linking up of small rays to form large ones takes place in older parts." This criticism does not appear valid, however, in view of the whole set of facts with regard to the seedlings of different groups of oaks accumulated by the American authors. According to the theory the "linking up" of uniseriate rays would begin in the later formed wood and gradually work back during descent into the earlier wood and into the seedling. And it is a significant fact that if we take the series: (1) seedlings of white oaks, (2) seedlings of black oaks, twigs of evergreen oaks, (3) adult wood of deciduous oaks in general, there is a general progression in the direction of compounding and the formation of broad rays in place of narrow ones.

Professor Groom also suggests that the linking of rays may be of physiological rather than phylogenetic significance. Is there any antagonism between the two? May not physiological factors (as indeed the American authors suggest) have been acting on the whole in a certain direction during the course of phylogeny, and thus brought about a gradual structural change in a corresponding direction, though with various fluctuations and digressions?

The facts with regard to Fagaceæ, mentioned by Groom and discussed by Thompson (5) certainly complicate the question, but the preliminary observations of Tabor, mentioned by Groom, seem rather to support the conclusions of Thompson (5) that there has, in several cases, been a splitting up of the broad rays into narrower ones.

Professor Groom shows an interesting general correlation between increase of the distinctness of the spring zone of large vessels and the replacement of narrow rays by broad ones. Both these phenomena are also apparently correlated, in a general way, with change from the evergreen to the deciduous habit.

The whole subject requires further investigation, and (we may add) fuller detailed description and illustration before we can arrive at a safe judgment on the theories put forward, but a fair *primâ facie* case may be said to have been established.

Some of the terminological suggestions of the American authors are not very happy. It is true no doubt that it is a mistake to call the broad rays of the oak *primary*, but it would scarcely be advisable to transfer the term to the narrow rays because they are thought to be primitive. It is much better to restrict the term primary to rays composed of primary tissue alone. This was pointed out many years ago by Scott, who tried to substitute the term *principal* for the broad rays separating the wedge-like masses of secondary xylem in various plants. Where the phylogenetic sequence of ray forms is well established the term *primitive* might be applied to a certain type of ray (*e.g.*, the uniseriate ones), but the term *uniseriate* has the merit of being accurately descriptive without implications. The term *multiseriate*, however, cannot reasonably be restricted to the narrower multiseriate rays merely because it is desired to separate them from the broad multiseriate rays, owing to a supposed difference of origin. The terms "broad" and "narrow" may be kept for the present: the word *compound* seems better applied to an aggregate of small rays which have not yet formed a completely homogeneous structure. A. G. T.